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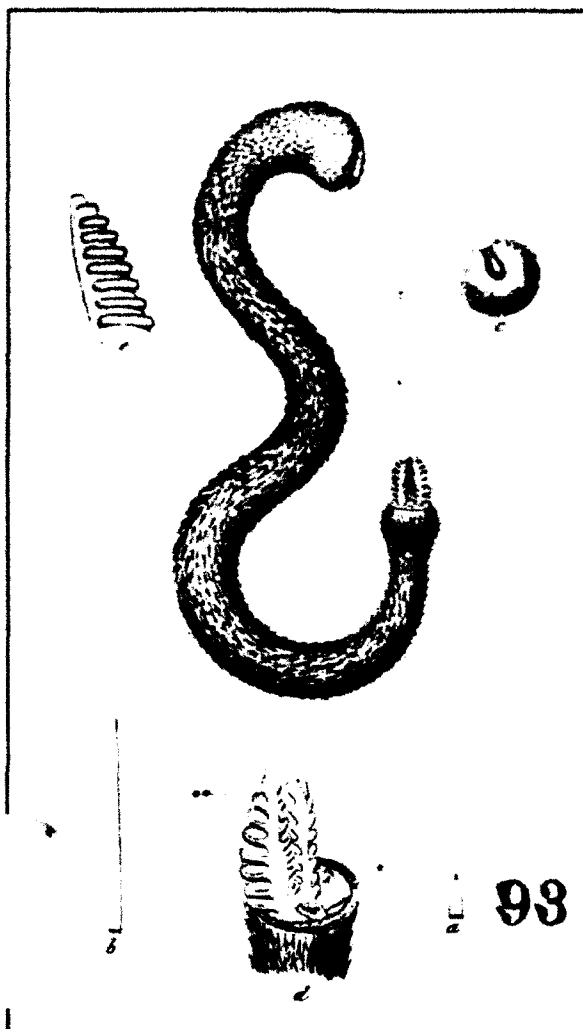
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***Chaetoderma nitidulum* Lovén 1844**

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**The Aplacophora: History, Taxonomy, Phylogeny,  
Biogeography and Ecology**

by

Amélie Hains Scheltema

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Woods Hole, Massachusetts 02543 USA

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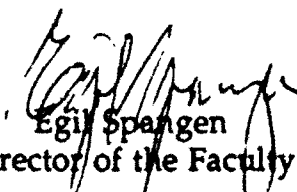

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**The Aplacophora: History, Taxonomy, Phylogeny,  
Biogeography and Ecology**

by

**Amélie Hains Scheltema, A.B. Bryn Mawr College**

**Woods Hole Oceanographic Institution  
Biology Department  
Woods Hole, Massachusetts 02543 USA**

**A Thesis Consisting of Thirteen Papers Published or in Press  
with Accompanying Text Submitted to the University of Oslo for Consideration  
as Partial Fulfillment of the Requirements for the  
Degree of Doctor Philosophiae**



**To Rudolf**

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# CONTENTS

	Page
Introduction .....	1
History .....	2
Classification .....	2
Collections .....	4
Aplacophora of Scandinavia .....	6
Taxonomy .....	9
Phylogenetic Considerations .....	13
Phylogeny of the radula .....	16
An alternative phylogeny .....	17
Biogeography and the Deep-Sea Fauna .....	19
Ecology .....	21
Future Directions for Research .....	22
Acknowledgments .....	23
References .....	25

## Appendices

A. Named Genera and Species of Neomeniomorpha .....	39
B. Named Genera and Species of Chaetodermomorpha .....	47
C. Aplacophorans Examined by A. Scheltema from Recent Atlantic Expeditions and Surveys .....	50
D. Major Expeditions and Surveys Which Have Collected Aplacophora in the Pacific .....	53
E. Preliminary Aplacophoran Identifications from One Expedition in the West European Basin .....	54
F. Characters Used for Descriptions of Aplacophora .....	60
G. Curriculum Vitae .....	63

## List of Tables

	Page
1. Classification of Aplacophora, 1844-Present .....	3
2. Two Classifications of Aplacophoran Molluscs in Current Use .....	5
3. Published Species of Aplacophoran Molluscs of Scandinavia .....	7
4. Published Species of Arctic and Sub-Arctic Aplacophora Not Reported from Scandinavia .....	8
5. Spicule Types in Families of Neomeniomorpha Ranked by Type of Radula .....	12

## List of Figures

1. Copy of original drawing of <i>Chaetoderma nitidulum</i> Lovén 1844 .....	69
2, 3. <i>Chaetoderma nitidulum</i> radula .....	71
4. Aplacophora collections from the Atlantic .....	73
5. Aplacophora collections from the Pacific .....	73
6. Spicules and copulatory spicules of two species of <i>Dorymenia</i> ; copulatory spicules of <i>Simrothiella margaritacea</i> (Kor. and Daniel.) .....	75
7. Spicules of two closely related species of aplacophorans under cross-polarized light .....	77
8. Radula types in Neomeniomorpha .....	79
9. Spicules and radulae of 7 species of <i>Helicoradomenia</i> from Pacific hydrothermal vents .....	81
10. A cladogram of molluscan relationships .....	83

## Included Papers Published or In Press as of April 1991

	Page
In press a. Scheltema, A. H. Class Aplacophora. <u>In</u> : Fauna of Australia. Bureau of Flora and Fauna Australian Dept. of Home Affairs and Environment, Canberra. (1990) .....	87
In press b. Scheltema, A. H., M. Tscherkassky and A. M. Kuzirian. Aplacophora. <u>In</u> : F. W. Harrison, ed., Microscopic Anatomy of Invertebrates. Wiley-Liss, Inc., New York. (1990) .....	125
1991 Scheltema, A. H. and A. M. Kuzirian. <i>Helicoradomenia juani</i> gen. et sp. nov., a Pacific hydrothermal vent Aplacophora (Mollusca, Neomeniomorpha). <i>Veliger</i> 34: 195-203. ....	197
1991 Scheltema, A. H., J. Buckland-Nicks and F.-S. Chia. <i>Chaetoderma argenteum</i> Heath, a northeastern Pacific aplacophoran mollusk redescribed (Chaetodermomorpha: Chaetodermatidae). <i>Veliger</i> 34: 204-213. ....	207
1990 Scheltema, A. H. Aplacophora as a Tethyan slope taxon: evidence from the Pacific. <i>Bulletin of Marine Science</i> 47: 50-61. ....	219
1990 Scheltema, A. H. and A. M. Kuzirian. The Aplacophora possess a true radular membrane. American Malacological Union Annual Meeting 3-8 June 1990, Woods Hole, Massachusetts. [Abstract.] ....	231
1989 Scheltema, A. H., K. Kerth, and A. M. Kuzirian. The primitive molluscan radula. <i>Unitas Malacologica</i> 10 <sup>th</sup> International Congress, 27 August to 2 September 1989, Tübingen, Germany. [Abstract.] ....	232
1989 Scheltema, A. H. Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off southeastern Australia. <i>Records of the Australian Museum</i> 41: 47-66. ....	233
1988 Scheltema, A. H. Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. <i>American Malacological Bulletin</i> 6: 57-68. ....	253
1987 Scheltema, A. H. Reproduction and rapid growth in a deep-sea aplacophoran mollusc, <i>Prochaetoderma yongei</i> . <i>Marine Ecology Progress Series</i> 37: 171-180. ....	265

## Included Papers Published or In Press as of April 1991 (Continued)

	Page
1985 Scheltema, A. H. The aplacophoran family Prochaetodermatidae in the North American Basin, including <i>Chevroderma</i> n.g. and <i>Spathoderma</i> n.g. (Mollusca, Chaetodermomorpha). Biological Bulletin (Woods Hole) 169: 484-529. ....	275
1981 Scheltema, A. H. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. Malacologia 20: 361-383. ....	321
1976 Scheltema, A. H. Two new species of <i>Chaetoderma</i> from off West Africa (Aplacophora, Chaetodermatidae). Journal of Molluscan Studies 42: 223-234. ....	345



## INTRODUCTION

The Aplacophora are a small class of benthic and epifaunal Mollusca found primarily at depths greater than 200 m throughout the world. They present zoologists with a unique set of questions that are treated in the several papers published or in press included herein (reference dates given in italics). The accompanying text expands on material in the papers and offers some new ideas that represent work in progress.

How can these vermiform molluscs covered with a spicular cuticle best be described so that they may be identified with some certainty by other than a specialist? The attempt to describe clear identifying characters has been made (Scheltema 1976, 1985, 1989 and *in press a*, Scheltema and Kuzirian 1991, Scheltema et al. 1991). Are Aplacophora primitive molluscs? and where do they fit phylogenetically in the phylum (Scheltema 1988)? What are the distinctive attributes of their anatomy (Scheltema 1981, *in press a*, Scheltema and Kuzirian 1991, Scheltema et al. *in press b*) and what are the homologies to other molluscs (Scheltema 1981, Scheltema et al. 1989, Scheltema and Kuzirian 1990, Scheltema et al. *in press b*)? What does their geographic distribution indicate about their history and origins in the deep sea (Scheltema 1990, *in press a*)? Are their life histories and their ecology unique adaptations to the deep sea (Scheltema 1987)?

An overall account of the class is presented in two recent papers (Scheltema *in press a*, Scheltema et al. *in press b*) and is not repeated here. An historical account, a catalogue of all aplacophoran collections known to me, and all published aplacophoran species is given in the following first section and appendices A-D. The second section on taxonomy emphasizes major characters and points to problems with the present classification. Questionable homologies and phylogenetic interpretations are given in the third section, and evidence that the class Aplacophora arose as the result of progenesis is presented followed by a new phylogenetic cladogram. The final two sections summarize the sparse existing knowledge on biogeography and ecology of this group.

The accompanying text does not represent an inclusive review of each subject covered. Just published as this thesis entered final typing is the splendid comprehensive volume by Gage and Tyler (1991) that brings together all aspects of deep-sea biology, most of which are only cursorily treated here in reference to the Aplacophora. The text that follows endeavors to tie my published works together within the framework of systematics in its broadest sense. All papers are from 1985 to the present except for two early ones included for continuity. Two of the recent papers are abstracts of work in progress.

## HISTORY

### Classification

The first aplacophoran mollusc reported in the literature, *Chaetoderma nitidulum*, was collected off the west coast of Sweden and described as an echinoderm (Lovén 1844) (Fig. 1). Its molluscan affinities were not suspected nor were anatomical studies undertaken for more than thirty years, although it was recorded in the literature as a sipunculid or priapulid by several authors (e.g., Diesing 1859, Keferstein 1865, Baird 1868) (Table 1). In 1875 a second species also from the west coast of Sweden, *Neomenia carinata*, was described through anatomical examination by Tullberg, who noted certain similarities to molluscs although a radula, character "par excellence" of molluscs, is lacking. (*Neomenia carinata* is perhaps a synonym of *Solenopus nitidulus* published as a *nomen nudum* by M. Sars [1869].) The next year the first anatomical description of *Chaetoderma nitidulum* was published, in which the derived radula with its large cone and two denticles was illustrated (Figs. 2, 3) (Graff 1876).

Subsequent to these two descriptions, a number of new species collected from Scandinavia by G. O. Sars were published without anatomical detail or figures (Koren and Danielssen 1877). These species awaited 40 years for adequate description (Odhner 1921) and more than 100 years for figures of the isolated radula and copulatory organs (Figs. 6, 8). Without knowledge of a typical radula, arguments raged over the systematic position of the Aplacophora, the discussions based on the published accounts of *Chaetoderma* and *Neomenia* by Graff and Tullberg. In one instance, *Neomenia carinata* was even redescribed from Tullberg's paper with posterior and anterior ends reversed (Kowalevsky and Marion 1882). Ihering (1877) placed the Aplacophora close to chitons in the phylum Amphineura because of the no longer held view that they resembled the worm-shaped *Cryptoplax*. Lankester (1877) believed *Neomenia* was like a generalized mollusc, but put it in a separate phylum Solecocomorpha. Hansen (1877), who examined *C. nitidulum* and corrected Graff's erroneous interpretation of the reproductive system, considered it to be near both annelids and molluscs. Gegenbaur (1878) was the first to bring *Chaetoderma* and *Neomenia* together in Vermes as Solenogastres, a name that continued to encompass both taxa for nearly a hundred years.

Finally in 1881 Spengel concluded that the Amphineura of Ihering contained both chitons and aplacophorans and that both are molluscs. His conclusions were based on a careful comparative study of the molluscan nervous system and included four species of aplacophorans. He noted, as well, that the "tongue" of *Chaetoderma* is a radula supported by two cartilages. Spengel's classification was accepted for Bronn's *Tierreich* as Class Amphineura with the orders Aplacophora (or Solenogastres) and Polyplacophora (Simroth 1892-1894). However, the great malacologist Thiele (1925), who had examined and described numerous aplacophoran species himself, continued to exclude the Aplacophora from the Mollusca but without placing them elsewhere. Furthermore he did not divide them into their two major taxa but merely ranked the family Chaetodermatidae equal and parallel with the families of neomenioids. Thiele's influence was broadened by H. Hoffmann (1929-30) who followed his arrangement accompanied by a lengthy argument in the new edition of Bronn.

Table 1. Classification of Aplacophora, 1844-present

Author	Supra Taxon	Phylum	Sub-phylum	Class	Sub-class	Order	Sub-order	Family or other
Lovén 1844	-	-	-	Echinodermata near Priapulid, Echiurid				Chaetoderma
Diering 1859	Vermes	-	-	-	-	Rhyngoda	-	Sipunculidea
Keferstein 1865	Vermes	-	-	-	-	Sipunculidea	-	Priapulacea
Baird 1868	Vermes	-	-	-	Gephyrea	-	-	Priapulidae
Sars 1869	Vermes	-	-	Gephyrea	-	-	-	Chaetoderma
	-	Mollusca <sup>1</sup>	-	Cephalophora	-	-	-	Solenopus (= Neomenia)
Lankester 1877	-	Mollusca <sup>1</sup>	Eucephala	Solecormorpha <sup>2</sup>	-	-	-	-
Ihering 1877	Vermes Amphineura <sup>3</sup>	-	-	Aplacophora	-	-	-	Chaetodermata, Neomeniidae
Gegenbaur 1878	Vermes Solenogastres	-	-	-	-	-	-	-
Spengel 1881	-	Mollusca	-	Amphineura <sup>3</sup>	-	-	-	-
Simroth 1892-94	-	Mollusca	-	Amphineura <sup>3</sup>	-	Aplacophora	Chaetodermatina Neomeniina	1 fam. 3 fam.
Pelsener 1906	-	Mollusca	-	Amphineura <sup>3</sup>	-	Aplacophora	Neomeniomorpha Chaetodermomorpha	-
Thiele 1925	-	-	-	-	-	-	-	Chaetodermatidae, Neomeniidae etc.
Hoffmann 1929-30	Vermes	-	-	-	-	-	-	4 fam.: Chaetodermatidae, Neomeniidae etc.
S. Hoffman 1949	-	Mollusca	-	Amphineura <sup>3</sup>	-	Solenogastres	Chaetodermatoidea Neomenioidea	-
Boettger 1956	-	Mollusca	Amphineura <sup>3</sup>	Aplacophora	-	Caudofoveata Ventroplicida	-	-
Hyman 1967	-	Mollusca	-	Aplacophora	-	Chaetodermatoidea Neomenioidea	-	1 fam. 3 fam.
Salvini-Plawen 1968b, 1969, 1978b	-	Mollusca	Aculifera <sup>3,4</sup>	Caudofoveata Solenogastres	-	1 ord. 4 ord.	-	3 fam. 18 fam.
Schelteema 1978	-	Mollusca	-	Aplacophora	Chaetodermomorpha Neomeniomorpha	-	-	-

1. The phylum Mollusca included Bryozoa, Brachiopods, and (Sars) tunicates.

2. Polyplacophora are not included.

3. Polyplacophora included

4. Subphylum Aculifera rejected by Salvini-Plawen 1985b

S. Hoffman (1949) again picked up the question of affinity of aplacophorans with molluscs. In a long account of the aplacophoran integument and homologies with chitons, Hoffman recognized the suborders Chaetodermatoidea and Neomenioidea as molluscs in the order Solenogastres, Class Amphineura. Boettger (1956) expanded on Hoffman's views, raised the order Solenogastres to Class Aplacophora, and renamed the two taxa as orders Caudofoveata and Ventroplicida. Hyman (1967) followed Boettger's classification but used Hoffman's terms Chaetodermatoidea and Neomenioidea as orders and rejected the concept Amphineura, which Boettger had retained as a "subclade".

Since 1967 Salvini-Plawen has published many new genera and species with anatomical descriptions. He has re-examined the position of Aplacophora within the Mollusca and concluded (1968b) that the two aplacophoran taxa are separate classes, the Caudofoveata and Solenogastres (see below, Phylogenetic considerations).

Two classifications are in current use, following Scheltema (1978) and Salvini-Plawen (1972b) (Table 2). Preferred here is Class Aplacophora, subclasses Chaetodermomorpha and Neomeniomorpha (the simpler -oidea endings are ordinal), with the subphyla Aculifera and Conchifera added (see section on Phylogeny). Pelseneer's (1906) names are retained for historical continuity, for despite name changes, there has been no change of group membership in the two taxa first recognized in *Chaetoderma* and *Neomenia*. The common terms chaetoderms and neomenioids used here apply to the two subclasses and solenogasters to the class. The most recent cladogram of Salvini-Plawen's (1985b) no longer recognizes the subphyla Aculifera and Conchifera.

## Collections

Interest in dredging sublittoral organisms gained momentum during the middle of the 19<sup>th</sup> century, partly in response to questions concerning whether there existed a depth below which no life existed (Scheltema and Scheltema 1972). Oceanic expeditions, as well as intensified collecting in the vicinity of European marine stations, brought a plethora of new species and higher taxa. Aplacophorans began to appear in increasing diversity at about the time that Spengel established them as molluscs. By 1880, most descriptions were based on histological sections. The descriptions of aplacophorans, authors, and geographic regions of these early dredge collections are: Mediterranean, Kowalevsky and Marion (1887), Kowalevsky (1901), Hubrecht (1888), Thiele (1894), Pruvot (1891, 1899), Wirén (1892b), and Nierstraz (1903, 1905); Scandinavia, Koren and Danielssen (1877) and Odhner (1921) (see also Table 3); Arctic and sub-Arctic, Wirén (1892a, b), Knipowitsch (1896), Thiele (1900, 1911, 1913b), and Derjugin (1915, 1928) (see also Table 4); Antarctic and sub-Antarctic, Pelseneer (1901), Nierstraz (1908), and Thiele (1913a); Indo-Pacific, Thiele (1897, 1902a,b, 1906) and Nierstrasz (1902); northwestern Atlantic, Wirén (1892b) and Heath (1912, 1918); and eastern and western Pacific, Heath (1904, 1905, 1911). In the numerous volumes of the great Challenger Expedition, which effectively showed that life exists at all depths in the ocean, there is described (poorly) a single species of Aplacophora (Selenka 1885), although Willemoes-Suhm (1876) described a living *Chaetoderma* in a letter, and a specimen is figured in Thomson's (1877) general account of the expedition. The

**Table 2. Two Classifications of Aplacophoran Molluscs  
in Current Use (from Scheltema 1978)**

APLACOPHORAN RELATIONSHIPS		101
TABLE 1. Classification of the living Mollusca. <sup>1</sup>		
I Phylum Mollusca	II Phylum Mollusca <sup>2</sup>	
Class Monoplacophora Wenz 1940	Subphylum Aculifera Metschek 1891 [= Amphineura von Ihering 1876]	
Class Aplacophora von Ihering 1876 [= Solenogastres Gegenbaur 1878]	Class Caudofoveata Boettger 1956	
Subclass Chaetodermomorpha Pelseneer 1906	Class Solenogastres Gegenbaur 1878 ( <i>partim</i> )	
Subclass Neomeniomorpha Pelseneer 1906 [= Ventr- pilicida Boettger 1956]	Class Placophora von Ihering 1876	
Class Polyplacophora (ex Polyplacophores) de Blainville 1816	Subphylum Conchifera	
(Classes Gastropoda, Pelecypoda, Scaphopoda, Cephalopoda)	Class Tryblidiida Wenz 1939 [= Monoplacophora]	
	(Classes Gastropoda, Bivalvia, Scaphopoda, Cephalopoda)	

<sup>1</sup>A recent classification including the extinct mollusks is in Runneger & Pojeta (1974), who place the Aplacophora and Polyplacophora by themselves in 2 separate subphyle.

<sup>2</sup>From Salvini-Plawen (1972).

latter probably received a formal description as *Metachaetoderma challengerii* Nierstrasz 1903, the sole and presently unknown species in the genus.

Following these early collections, which were taken mostly with coarse-mesh sledges between about 1860 and World War I, only a few new species of aplacophorans from the Atlantic, Mediterranean, and Japan were published (Lummel 1930, Leloup 1950, Baba 1939, 1940a). Renewed interest in the deep-sea benthos began in the late 1940s with the Russian explorations of hadal depths (Belyaev 1989) and in 1950-52 with the Danish Galathea Expedition. By the end of 1960, the use of precision depth recorders, epibenthic sleds (Ockelman 1964, Hessler and Sanders 1967), and small-mesh screens assured capture and retention of small organisms from all depths. Since 1969 spade box corers of usually 1/4 m<sup>2</sup> have provided quantitative samples of nearly undisturbed sediment (Hessler and Jumars 1974). Collections are now also made from research submarines, providing samples from hard surfaces such as those surrounding hydrothermal vents (Scheltema and Kuzirian 1991) or from guyots which are otherwise impossible to sample.

Published surveys made since 1950 that sampled Aplacophora include: Eastern Pacific (Schwabl 1963, Salvini-Plawen 1972a, 1978b; Scheltema 1985a, Osorio and Tarifeño 1976), Antarctic and sub-Antarctic (Kaiser 1976, Salvini-Plawen 1978b), Australia and New Zealand (Ponder 1970, Scheltema 1989), Atlantic (Salvini-Plawen 1968a, 1971, 1972a, 1977a, 1978a, Scheltema 1976, 1985a, b), Mediterranean and Red Sea (Salvini-Plawen 1969, 1972a, 1977a, b), Scandinavia (see Table 3), Sea of Japan and off Japan (Okuda 1943, Baba 1975, Ivanov 1984), and Arctic and sub-Arctic (Ivanov 1981, Knudsen 1949 and Table 4). New techniques for extracting meiofauna from the sediment (Hulings and Gray 1971, Morse and Scheltema 1988) have brought several Aplacophora to light (Morse 1979, Salvini-Plawen 1968c, 1985a, 1988). Collections exist from other surveys that await descriptions of the Aplacophora (Figs. 4, 5; Appendices C, D).

### Aplacophora of Scandinavia

Seventeen neomenioid and 7 chaetoderm species have been described from the coast of Scandinavia both above and below the Arctic Circle (Table 3). Two additional neomenioids and 13 chaetoderms described from the Arctic and sub-Arctic have not been reported from Scandinavia but perhaps some may occur there (Table 4). Aplacophorans collected by early Scandinavian expeditions to the Norwegian Sea and North Atlantic -- the Norwegian North Atlantic Expedition 1876-78 and the Danish Ingolf Expedition 1895-96 -- were described by Odhner (1921) and Salvini-Plawen (1971, 1975). Aplacophorans from the 1975 Swedish-French expedition NORBI to the Norwegian Sea have still to be published (Bouchet and Warén 1979).

Table 3. Published Species of Aplacophoran Molluscs of Scandinavia  
(A = Arctic only; S = south of Arctic Circle only;  
AS = Arctic and south of Arctic Circle)

Species	Distribution	Reference No. <sup>1</sup>
<b>Neomeniomorpha</b>		
<i>Aesthoherpia glandulosa</i> Salv.-Pl.	S	8
<i>A. gonoconota</i> Salv.-Pl.	S	8
<i>Alexandromenia crassa</i> Odhner	S	1
<i>Anamenia borealis</i> (Kor. & Daniel.)	AS	1, 12
<i>Dorymenia sarsii</i> (Kor. & Daniel.)	AS	1, 12
<i>Drepanomenia incrustata</i> (Kor. & Daniel.)	A	1, 12
<i>Genitoconia rosa</i> Salv.-Pl.	S	2
<i>G. atriolonga</i> Salv.-Pl.	S	2
<i>Gymnomenia pellucida</i> Odhner	S	1
<i>Kruppomenia borealis</i> Odhner	S	1, 10
<i>Micromenia fodiens</i> (Schwabl)	S	8, 11
<i>Nematomenia norvegica</i> Odhner	S	1
<i>Neomenia carinata</i> Tullberg	S	1, 12
<i>Neomenia dalyelli</i> (Kor. & Daniel.)	A	1, 12
<i>Proneomenia sluiteri</i> Hubrecht	A	1, 12
<i>Simrothiella margaritacea</i> (Kor. & Daniel.)	S	1, 10
<i>Wierenia argentea</i> (Odhner)	S	1, 8
<b>Chaetodermomorpha</b>		
<i>Chaetoderma intermedium</i> Knipowitsch	AS	4, 5, 6, 7
<i>C. nitidulum</i> Lovén	AS	1, 3, 4, 6, 7, 9, 12
<i>Falcidens crossotus</i> Salv.-Pl.	AS	3, 4, 6, 9
<i>F. sagittiferus</i> Salv.-Pl.	AS	3, 4, 6, 9
<i>F. sterreri</i> Salv.-Pl.	S	2, 4, 6, 9
<i>Scutopus robustus</i> Salv.-Pl.	S	4, 6, 9
<i>S. ventrolineatus</i> Salv.-Pl.	AS	3, 4, 6, 9

#### References

1. Odhner 1921
2. Salvini-Plawen 1967
3. Salvini-Plawen 1968a
4. Salvini-Plawen 1970
5. Salvini-Plawen 1971
6. Salvini-Plawen 1975
7. Salvini-Plawen 1978a
8. Salvini-Plawen 1988
9. Salvini-Plawen & Warén 1972
10. Scheltema & Kuzirian 1991
1. Schwabl 1955
2. Thiele 1932

**Table 4. Published Species of Arctic and Sub-Arctic Aplacophora  
Not Reported from Scandinavia**

Species	Reference No. <sup>1</sup>
<b>Neomeniomorpha</b>	
<i>Nematomenia arctica</i> Thiele	7
<i>Syngenoherpia</i> (?) <i>thulensis</i> Thiele	7
<b>Chaetodermomorpha</b>	
<i>Caudofoveatus tetradens</i> Ivanov	2
<i>Chaetoderma chistikovi</i> (Ivanov)	1, 6
<i>C. glacialis</i> (Ivanov)	1, 6
<i>C. luitfriedi</i> (Ivanov)	2, 6
<i>C. marinae</i> (Ivanov)	2, 6
<i>C. pellucida</i> (Ivanov)	2, 6
<i>C. productum</i> Wirén	3, 4, 5, 7
<i>C. simplex</i> Salv.-Pl.	4, 5
<i>Falcidens afanasjevi</i> (Ivanov)	1, 6
<i>F. ingolfensis</i> Salv.-Pl.	4, 5
<i>F. moskalevi</i> (Ivanov)	1, 6
<i>F. profundus</i> Salv.-Pl.	4, 5
<i>F. thorensis</i> Salv.-Pl.	4, 5

<sup>1</sup>References

1. Ivanov 1986
2. Ivanov 1987
3. Salvini-Plawen 1970
4. Salvini-Plawen 1971
5. Salvini-Plawen 1975
6. Salvini-Plawen 1984
7. Thiele 1932



## TAXONOMY

Traditionally, before large collections containing many specimens of a species were available, aplacophorans were described by a few spicules drawn at small size, a small drawing of a specimen, and histologic sections (see, e.g., Nierstrasz 1902, Heath 1911, 1918). Only Kowalevsky (1901) drew radulae which had been isolated by dissolving the surrounding tissue. In the neomenioids, presence or absence of copulatory spicules was noted and sometimes cross-sections of dissolved spicules were drawn from histological sections, but they were never isolated intact. Many species have been described from a single specimen (see Appendices A, B) and thus the holotype if it exists is only as sectioned material. Syntypes, if extant, have often lost their spicules through poor preservation. If an author has had forethought, a slide was made of dislodged spicules before the animal was sectioned (e.g., Heath species in Scheltema et al. 1991) or only anterior and posterior ends were sectioned, leaving the mid-section complete with spicules (e.g., *Dorymenia sarsii* [Kor. & Daniel.]). In one instance the type of a Heath species, *Chaetoderma robustum*, was even deposited in two museums, the histologic sections of each end in one, the mid-section in another.

Details of the methods now used in describing Aplacophora are found in the following papers included herein: for chaetoderms, Scheltema (1976, 1985, 1989) and Scheltema et al. (1991); for neomenioids, Scheltema and Kuzirian (1991); and for both chaetoderms and neomenioids, Scheltema (*in press a*). The general anatomy of both taxa are given in Scheltema (*in press a*) and Scheltema et al. (*in press b*). Recent descriptions rely on characteristics and measurements of the entire body and on the morphology of hard parts: epidermal spicules, radula, and copulatory spicules if present. Body measurements and ratios often allow species to be distinguished and make statistical comparison among populations possible (Scheltema 1985). The use of an image analysis system affords new possibilities for more precise measurements and a preliminary trial has shown its use to be applicable to small aplacophorans.

There is often more than one type of spicule present within a single specimen of a species (see e.g., Scheltema 1989, Scheltema et al. *in press b* Figs. 3C, D). Spicule morphology falls into broad categories: flat-lying solid scales or leaf-like plates, solid or hollow spicules of various shapes held upright in the cuticle, and, in many neomenioids, solid or hollow skeletal spicules, often S-shaped, that lie within the cuticle and cross each other at a 90° angle, running ventroanterior to dorsoposterior and dorsoanterior to ventroposterior, forming a strong, reticulated network. Spicules drawn at a reasonably large scale of 400X from particular regions along the length of the body can be used for distinguishing species, and their measurements can serve to differentiate closely related forms. For instance, a comparison of the spicules of two nearly indistinguishable *Dorymenia* species, *D. sarsii* and a new species to be published, indicates separation partly on the basis of the small, solid, paddle-shaped spicules which are few and rounded in *D. sarsii* and many and pointed in *D. sp.* (Fig. 6E,F) and on the greater width of hollow skeletal spicules in *D. sarsii* (14-20 µm) compared to *D. sp.* (9-18 µm).

Spicule sculpturing, which is prevalent among chaetoderms, distinguishes species and can be used as a generic character, e.g., a medial groove defines the genus *Chevroderma* (Fig. 7) and crossed ridges will be used to separate a group of *Falcidens* species into a new genus (Scheltema 1989, 1990).

Because spicules are formed of aragonite crystals aligned with the long axis, cross-polarized light produces birefringent colors in solid spicules. The boundaries between color bands, or isochromes, indicate where a spicule is thickest and thus the pattern of thickening. This character is useful in distinguishing *Chevroderma turnerae* from *C. gausson* and indicates that spicules in the genus *Chevroderma* are asymmetrical (Scheltema 1985) (Fig. 7). In *Chaetoderma argenteum* the inverted V-shaped pattern of thickening in anterior trunk spicules separates this species from other closely related eastern Pacific species and provides a basis for synonymy (Scheltema et al. 1991).

Scanning electron microscopy gives a three-dimensional view showing spicule curvature and sculpturing (e.g., Scheltema 1985 Fig. 4F, 1989 Fig. 2, Scheltema et al. 1991 Fig. 5E). Finally, the manner in which spicules are held on the body is a useful distinguishing character, particularly in preliminary sorting of samples (e.g., Scheltema et al. *in press b* Fig. 3A, B, Scheltema 1989) (see Appendix E).

As in other molluscs the radula provides an important taxonomic character, but it is lacking in 19 percent of neomenioid genera. Small differences found in isolated radulae from morphologically similar species are consistent (e.g., Fig. 8J, K, *Dorymenia sarsii* and *D. sp.*; Scheltema 1989 Fig. 9, *Falcidens loveni* and *F. chistos*). These differences usually cannot be distinguished in histological sections.

Copulatory spicules and spicules accessory to them in the mantle cavity wall are present in many Neomeniomorpha and serve to distinguish very similar species (see Fig. 6C, D for *Dorymenia sarsii* and *D. sp.*). In some species copulatory spicules are apparently deciduous and their absence may be temporary, so presence or absence of copulatory spicules is not a character that can be used solely for differentiating either species or genera. For instance, in descriptions of *Proneomenia* and *Dorymenia* the only character difference noted between the two genera is presence or absence of copulatory spicules (e.g., Salvini-Plawen 1978b), but in *D. sarsii* the copulatory spicules may be either absent or present, and in *D. sp.* they were found in different stages of development in different specimens (Fig. 6A, B). *Dorymenia* is therefore probably a synonym of *Proneomenia*.

Hard parts and body shape are adequate for placing Chaetodermomorpha into higher taxa. The radula in particular defines genera and families (Salvini-Plawen 1969). The classification is quite stable, although the final generic placement of certain groups of species still needs to be determined (see above).

The systematic situation is far different in the Neomeniomorpha, in which the status of genera and higher taxa remains in a state of flux. Hard parts and body shape alone may be adequate

to define genera, but so far published descriptions are too incomplete to be able to judge adequacy. Neomenioids should be sectioned and stained with a trichrome stain to discover several important soft anatomical characters, in particular morphology of salivary glands, reproductive tract, and epidermal glands (e.g., Scheltema and Kuzirian 1991, Scheltema et al. *in press b*). In some cases the radula is useful in defining families or perhaps orders (e.g., Simrothiellidae, Scheltema and Kuzirian 1991), but certain radular types occur in taxa with otherwise very disparate characters. Table 5 gives spicule types for families grouped by the radula types shown in Figure 8. Without further information it cannot be determined whether spicule type, radula type, or both are polyphyletic characters. Certainly neither character alone can serve for higher classification. Thus the grouping of Neomeniomorpha into four orders on the basis of the closely linked, nonindependent characters of cuticle thickness, type of integumental spicules, and presence or absence of epidermal papillae has led to polyphyletic groups (Salvini-Plawen 1978b, Boss 1982). In one instance, genera with fishhook-shaped spicules were placed into 2 orders depending on whether the spicules were solid (*Ocheyoherpia*) or hollow (*Pararrhopalia*, *Eleutheromenia*). Furthermore, the thickness of the cuticle in a new species of *Ocheyoherpia* shows inconstancy of this character even within a genus (*Ocheyoherpia lituifera*, 56  $\mu\text{m}$ , "thick"; *Ocheyoherpia* sp., 22  $\mu\text{m}$ , "thin"; unpublished). In another instance, ordinal lines based on spicule type are crossed by genera with the closely related morphologies of a denticulate bar radula and paired anteroventral radular pockets (*Helicoradomenia*, solid spicules; *Kruppomenia*, *Simrothiella* s.s., and "*Simrothiella*" [Salvini-Plawen 1978b] [a new genus], hollow spicules) (Scheltema and Kuzirian 1991).

Similarity in the morphology of copulatory spicules may prove to be the result of parallel evolution in closely related species. Figure 9 indicates the situation in 7 species of the hydrothermal vent genus *Helicoradomenia*, in which the evolutionary relationships among species cannot be determined from copulatory spicules alone.

The present classification of Neomeniomorpha is in need of radical revision. Recently collected species of poorly known genera are now providing material for re-examination (e.g., *Archaeomenia*, *Acanthomenia*, *Kruppomenia*, several species of Pararrhopalidae, *Macellomenia*, *Uncimenia*; see Appendix E). With enough new information, cladistic analysis should help decide which character states represent monophyly and which are due to homoplasy. A list of characters considered for each subclass is found in Appendix F.

The use of ventral salivary glands in the taxonomy of Neomeniomorpha also needs to be noted. These glands have been divided into 4 types on putative differences in the relationship of the gland cells to epithelium and underlying connective tissue or muscle (see Salvini-Plawen 1978b, 1985b p. 88). The type of salivary gland has then been used for familial classification. However, Volker Storch and I have closely examined several of the same families and genera described by Salvini-Plawen and we find only morphological variation of the type termed "simple exoepithelial glands" (Welsch and Storch 1973), that is, glands formed by tubular invaginations of the epithelium into the underlying connective tissue (examples are shown in Scheltema et al. *in press b* Figs. 13B, 20A and in Scheltema and Kuzirian 1991 Fig. 4C). The validity of using ventral salivary gland morphology for classification above the generic level has still to be tested.

**Table 5. Spicule Types in Families of Neomeniomorpha Ranked by Type of Radula (cf. Fig. 8)**

Radula type	Family	Solid scales	Solid upright	Solid skeletal	Hollow upright	Hollow skeletal
Distichous denticulate hooks	Gymnomeniidae	+				
	Lepidomeniidae	+				
	Phyllomeniidae		+	+		
	Heteroherpidae			+		
	Pararrhopalidae		+		+	+
	Epimeniidae					+
Distichous denticulate bars or pectinate bars	Simrothiellidae		+		+	+
Monostichous pectinate bar	Macellomeniidae	+	+			
	? Sandalomeniidae	+				
Monostichous, denticles not fused	Amphimeniidae					+
Monostichous, denticles fused	Dondersiidae	+				
	Acanthomeniidae		+		+	
Polystichous	Hemimeniidae		+			
	? Imeroherpidae		?	?		
	Proneomeniidae		+			+
	Strophomeniidae					+
	Rhipidoherpia					+

## PHYLOGENETIC CONSIDERATIONS

The uniqueness of Aplacophora among the Mollusca lies in their highly derived vermiform body which surrounds an internal organization that appears to reflect a primitive molluscan state, especially the simple ladderlike nervous system, a distichous radula (2 teeth per row) in its plesiomorphic aplacophoran state, and an aculiferous cuticle. Both historically and recently the Aplacophora have been considered closely related to the Polyplacophora because of similarities in the plan of a ladderlike nervous system (Amphineura) or spicular cuticle (Aculifera).

Much has been written by Salvini-Plawen on the importance of Aplacophora to understanding the evolution of molluscs so that little doubt remains about the substantial significance of this group in molluscan phylogeny. Most importantly the Hypothetical Ancestral Mollusc (HAM), with its agglomeration of various characters chosen from among the classes, has been brought to extinction and has been replaced by a hypothetical ancestor that can fill the requirements of cladistic analysis (cf. Stasek 1972). Salvini-Plawen's several papers (especially 1972b, 1981 emended 1985b) conclude that (1) molluscs arose from an acoelomate turbellariomorph; (2) chaetoderms are the sister group (scutopods) to all other molluscs (adenopods); (3) the (nonexistent) adenopod ancestor gave rise to neomenioids which are the sister group to all remaining molluscs (testaria); (4) the Polyplacophora, whose eight shell plates were formed by fused spicules, are the sister group to the shelled molluscs without spicules, the Conchifera, whose shells were evolved by fusion of chiton plates (see Scheltema 1988 Fig. 1).

I have questioned some of the arguments and homologies that allow such a phylogenetic structure (1988). (1) The "primitive" classes Monoplacophora, Aplacophora, and Polyplacophora all have large pericardial (coelomic) spaces relative to other molluscs, which argues for the presence of a coelom in the archimollusc and a reduction of coelom in the "higher" molluscs (Scheltema 1988 Fig. 13). Recent sequencing of ribosomal RNA among 22 classes (not including Aplacophora) in 10 animal phyla splits off the acoelomate Platyhelminthes from all the eucoelomate taxa. The eucoelomates fall into 4 closely branched groups, an argument for a single origin of the coelom (Field et al. 1988). Thus an independent acoelomate turbellariomorph ancestry for molluscs is not supported by either morphological or biochemical evidence.

(2) The homology of the chaetoderm oral shield with the foot of chitons (S. Hoffman 1949), both said to have evolved from the creeping sole of the archimollusc, formed the basis for separating the two aplacophoran taxa into two classes. This homology is not upheld by either light or transmission electron microscopy (Scheltema 1988 Figs. 5,6, Scheltema et al. *in press* b Fig. 9, Tscherkassky 1989). Thus (3) there is no "adenopod" and the two aplacophoran taxa belong together in a single class, sharing the apomorphy of a worm shape.

(4) The shell plates of Polyplacophora are not formed by fusion of calcium carbonate granules and are not homologous to the shells of other molluscs based on either their ontogeny (Kniprath 1980, Eyster and Morse 1984 in Scheltema 1988 Fig. 4) or shell structure, for the hypostracum acts crystallographically as a single crystal (Haas 1977, 1981 in Scheltema 1988 p. 60). The

results of rRNA sequencing brought Mollusca, Annelida, Brachiopoda, Pogonophora, and Sipuncula together in the eucoelomate protostome group (Field et al. 1988). rRNA was sequenced from four molluscs: 2 clams, a nudibranch, and a chiton. The nudibranch branches off closely but separately from the clams. The chiton does not branch with the clams but is closest to the Annelida, Brachiopoda, and Pogonophora, although the exact order of branching is uncertain (Field et al. 1988 p. 750). Thus, based on three separate pieces of evidence — shell structure, shell ontogeny, and biochemistry — chitons should not be closely linked to other shelled molluscs.

I first postulated elsewhere that the Aplacophora are the sister group to all other molluscs (Scheltema 1988 Fig. 14) without considering this basic question: Why — or how — did a mollusc acquire a derived worm shape while still retaining plesiomorphic characters? There are two possible answers: (1) the new character "vermiform" was added to the adult of a pre-existing primitive aculiferous species or (2) a worm shape came about through heterochrony, i.e., progenesis, and the apparent primitiveness of organ systems is the retention of juvenile (i.e., ancestral ontogenetic) states in an adult form. The first possibility, although not directly stated by him, is the underlying assumption of the phylogenetic cladogram by Salvini-Plawen (1972b, 1981). The second possibility, that of progenesis, has not yet been explored in print but was first proposed by David R. Lindberg in a talk presented at meetings of The Paleontological Society (1985, Orlando, Florida). Some evidence supporting the hypothesis that heterochrony was the evolutionary process that produced Aplacophora are presented here. The terminology follows Gould (1977): progenesis is the retention of ancestral juvenile characters in an adult form through acceleration of sexual maturation. Neoteny also results in retention of juvenile characters in a descendant adult, but through retardation of somatic development. Both progenesis and neoteny are forms of paedomorphosis.

(1) A worm shape can be achieved by elongation of an embryo early in ontogeny.

(2) Narrowing a body by the addition of a worm shape to a pre-existing adult body should be reflected in some manner in the internal anatomy, and the more elongate the shape, the more pronounced should internal changes become. Within the Neomeniomorpha there is little organizational difference in the anterior and posterior ends or in musculature between short and elongate species; elongation of the external form is usually accompanied internally by simply lengthening the gonad and midgut. A notable exception is the derived family Dondersiidae, which possesses a monostichous radula and unpaired copulatory spicules. The situation in chaetoderms is different and does not serve the argument. The Chaetodermomorpha as a whole are adapted for burrowing and appear to be derived from the Neomeniomorpha, with fusion of the nervous system, loss of the foot, loss of dorsoventral musculature, and specializations of the gut.

Chitons are generally agreed to be the closest relatives of the Aplacophora (spicules, mantle groove, nervous system) and can be studied for homologies and analogies. In *Cryptoplax*, a genus of chiton with a derived worm shape, there are at least four specializations of adult characters: (a) the mantle is very thick relative to the internal body diameter; (b) there is loss of

circulatory pathways; (c) there is loss of shell and shell musculature; and (d) the intestinal tract is remarkably long and complicated, turning back on itself in numerous spirals (Weustein 1904, Hoffmann 1929-30).

There appears to be a clear ontogenetic difference in the evolutionary pathways to worm shape taken by these two aculiferan taxa, Aplacophora and *Cryptoplax*. The differences are hypothesized to be due to heterochrony for the former and addition to an existing adult sequence in the latter.

(3) Progenesis results in loss of temporal genetic regulation and pathways in later stages of ontogeny and usually does not lead to progressive evolution; that is, there is less genetic expression for selection to act upon. The Aplacophora are a small taxon with little variability although they inhabit the enormous space of the world's oceans from sublittoral to hadal depths. This lack of variability is interpreted to be the result of progenesis. On the other hand chitons are also a relatively small taxon among Mollusca with little variability, but they seem to demonstrate the result of adaptation to a spatially limited habitat, the littoral and sublittoral hard rocky substrate to which they are mostly restricted, rather than loss of genetic transformation through progenesis.

(4) As a process, progenesis results in early reproduction and reduction in body size (Gould 1977). One abundant aplacophoran species living at 2000 m is known to mature within one year and is interpreted as being an opportunistic species (Scheltema 1987). Life histories for all other Aplacophora remain unknown and thus early reproduction may not be the usual case in extant species. Body size is small in most aplacophorans, with length usually less than 5 mm. Like some other deep-sea taxa such as protobranch bivalves (Sanders and Allen 1973) and isopods (Hessler et al. 1979), aplacophorans have evolved primarily in the deep sea, where food is limiting and small size of the macrobenthos is the norm (Monniot and Monniot 1978, Allen 1983, Soetaert and Heip 1989). A reduced size and early maturation through progenesis might have pre-adapted a shallow-water ancestral mollusc for colonizing the continental slope, or such an evolutionary event could have arisen after an early ancestor had already migrated into the deep sea. Perhaps an early aculiferan, outcompeted by the rapidly diversifying Conchifera, took refuge on the continental slope, where diminished food encouraged smaller size and early maturation. Large aplacophorans do exist in the deep sea, but they are usually either specialized (giant *Neomenia* species, Baba 1975, Kaiser 1976) or live in environments where food is not limiting (e.g., high latitudes; *Proneomenia sluiteri*, Derjugin 1915, 1928). Other large neomenioid species from abyssal depths which are still to be described may have a unique feeding type (see Monniot and Monniot 1978 for tunicates) or be capable of covering a larger foraging area (Soetaert and Heip 1989). I consider that large body size in the Aplacophora is an apomorphic character because it is found scattered amongst unrelated families, some of which, like the Neomeniidae, are highly derived.

Progenesis has not been a universal process for deep-sea organisms, e.g., deep-sea isopods have specialized from more primitive shallow-water forms (Hessler et al. 1979) as have asteroides (Madsen 1961), but it has occurred in other groups (e.g. elaspod holothurians, Hansen 1975, and

several tunicate genera, Monniot and Monniot 1978). Progenesis as a general evolutionary process among deep-sea taxa has not been explored.

(5) Certain character states in the Aplacophora can be interpreted as being less developed through progenesis than the states in homologous characters of other molluscs, e.g., the simple organic composition of the cuticle (Beedham and Trueman 1968); the small posterior mantle cavity that serves as little more than a cloaca; the circulatory system consisting only of heart, aorta, and open sinuses; lack of kidneys; a foot as a ciliated ridge without musculature; and the joining of gonads and pericardium that reflects the early ontogenetic state in chitons (Hammarsten and Runnström 1925, Fig. Q).

Although the five lines of evidence for progenesis presented here can argue for heterochrony in the Aplacophora, they cannot be tested either against fossils, which do not exist, or against a more complete phyletic lineage as has been done for progenetic meiofaunal forms (Westheide 1987) and deep-sea tunicates (Monniot and Monniot 1978). Nevertheless, the possibility remains that Aplacophora may be progenetic rather than primitive with two important consequences: (1) aplacophoran organ systems are not primitive but can serve as models of a primitive molluscan state and (2) the Aplacophora are not the taxon closest to the stem form in the phylogeny of molluscs. The first point can be illustrated by a brief description of the radula as a model organ system for the ancestral molluscan state. A new phylogenetic cladogram follows which proposes a metameric, nonaculiferous archimollusc as the stem form.

### Phylogeny of the radula

The radula in aplacophorans has been shown by microscopy to be produced in the same way as in other molluscs: odontoblasts at the blind end of a radular sac produce teeth sequentially; the teeth are then attached to a radular membrane produced by membranoblasts adjacent to the odontoblasts (light microscopy, Scheltema et al. *in press b* Fig. 17D, Scheltema and Kuzirian 1990; transmission electron microscopy, K. Wolter in manuscript and personal communication). The teeth and membrane are formed of  $\alpha$ -chitin (K. M. Rudall, in litt.). The teeth on the membrane are apparently carried forward, and many aplacophorans retain some or all of the radula in an anteroventral pocket or paired pockets so that the entire ontogeny of the radula is preserved (e.g. *Simrothiella*, Fig. 8C herein; *Helicoradomenia* sp., Scheltema 1988 Fig. 8A, B). The aplacophoran radula has rows of 2 teeth (distichous), 1 tooth (monostichous), or 4 or more teeth (polystichous) (Fig. 8). The distichous denticulate bar has been determined to be the plesiomorphic type on the basis of ventral salivary gland morphology and comparison with the ontogeny of chiton and gastropod radulae (Scheltema et al. 1989). However, Ivanov (1990) gives a much different view, considering the monostichous radula shown in Fig. 8F as plesiomorphic. Because all monostichous radulae are associated with derived ventral salivary glands — single rather than paired ducts, or ducts as ampullae — this view seems incorrect. If we take the plesiomorphic aplacophoran distichous bar as a model for the primitive state of the molluscan radula, we can consider that the archimollusc had a radular membrane, perhaps paired, to which were attached along their entire width paired single denticulate teeth in repeated rows, and the process of radula formation was genetically fixed. Morphologically similar teeth in two or three



rows are found in the Cambrian Burgess Shale fossil *Wiwaxia* (Conway Morris 1985), which has recently been placed in the Annelida (Butterfield 1990). Whatever the phylogenetic affinities of *Wiwaxia*, such radular-like teeth (surely not jaws) may have ancient, premolluscan beginnings.

Interestingly, the plesiomorphic aplacophoran radula is found in its most generalized, i.e. primitive, state in the hydrothermal vent genus *Helicoradomenia* (Scheltema and Kuzirian 1991). Other vent taxa also have primitive characters and are perhaps relicts of earlier ages (Newman 1985).

### An alternative phylogeny

The ancestral mollusc at the base of the cladogram in Figure 10 is considered to have the following plesiomorphies: (1) small size (Cambrian Mollusca, Runnegar and Pojeta 1985); (2) metamerism, perhaps 8-fold, including paired dorsoventral muscles, nephridia, gonopores, hearts (Monoplacophora, Lemche and Wingstrand 1959; serial ostia, Polyplacophora); (3) distichous radula (Aplacophora, ontogeny of some Gastropoda and some Polyplacophora, Scheltema, Kerth, and Kuzirian 1989 and in progress); (4) coelom including paired pericardial cavities (Monoplacophora, fused but large in Aplacophora and Polyplacophora, Scheltema 1988; rRNA sequencing, Field et al. 1988); (5) dorsal cuticle (Aplacophora and Polyplacophora; doubtfully homologous with periostracum); (6) ventral ciliated locomotory sole and pedal mucous gland (Mollusca generally, pedal gland sometimes in early ontogeny only); (7) extracellular  $\text{CaCO}_3$  deposition by dorsal epidermis (Mollusca generally); (8) nervous system with cerebral ganglia and commissure, circumenteric ring, paired lateral and pedal cords with cross-commissures and posterior connection (Monoplacophora, Aplacophora and Polyplacophora, but in the latter two only the lateral cords are united posteriorly); (9) head separate from locomotory sole (Mollusca generally); (10) a one-way gut with mouth/anus, and with stomach and digestive gland poorly differentiated or separated (Neomeniomorpha, Monoplacophora, see Wingstrand 1985, figs. 13, 14, Pl. 7 figs. 24, 25); and a groove between the dorsal and ventral surfaces, the future mantle cavity (Mollusca generally). The  $\text{CaCO}_3$  deposits served to stiffen the cuticle but did not form an external cover, and they were not organized into either spicules or shell. Crustacean cuticle offers an analog.

Two major evolutionary directions are involved in the method by which  $\text{CaCO}_3$  deposits became the external molluscan covering. In the Conchifera, which were already present in the Early Cambrian, calcium deposition takes place by transport from the epithelial tissue into an open, fluid-filled space between the mantle and periostracum. It originates in the embryonic shell-field invagination (Eyster and Morse 1984). The Conchifera include all fossil and extant molluscs other than the Polyplacophora and Aplacophora. In the Aculifera (Polyplacophora and Aplacophora) single spicules of  $\text{CaCO}_3$  are deposited within invaginations of individual epithelial cells; in Polyplacophora the large spines are produced by a proliferation of the original cell (Haas 1981). The spicules are pushed into and usually beyond the cuticle. Both processes of  $\text{CaCO}_3$  deposition result from very precise organization under strict genetic control as shown by the intraspecific integrity in shape of both shells and spicules.

After the Conchifera diverged from the stem line, the mantle deepened and gills developed. Metamery was retained in the Monoplacophora but lost in the rest of the Conchifera, except for dorsoventral (pedal) musculature in some taxa and the renal system in cephalopods. The Aculifera may have evolved either at the same time as the Conchifera or later. By the Upper Cambrian or Lower Ordovician, the serial shell plates of the Polyplacophora had evolved (Runnegar and Pojeta 1985). This event was preceded by an increase in size of an early aculiferan to accommodate the shell plates. In the separate evolutionary event of progenesis, the Aplacophora evolved with reduction in size, loss of metamery and nephridia, retention of the gonad-pericardial connection, and acquisition of a worm shape. The Chaetodermomorpha were derived from the neomenioid-like stem with complete loss of foot, reduction in the nervous system, and specializations of the gut.

This phylogenetic cladogram does not call for fusing  $\text{CaCO}_3$  deposits or for evolving the clearly primitive and metameric Monoplacophora after Aplacophora and Polyplacophora. If known fossils reflect the actual time of evolutionary events, then the evolution of Polyplacophora late in the Cambrian (Runnegar and Pojeta 1985) from a continuing line of aculiferous creatures was probable, with increased size and muscles being the determinants of shell plates rather than vice-versa (see Hammarsten and Runnström 1925, p. 276, for ontogenetic development of muscle before shell). The Aplacophora, with their highly derived shape and paedomorphic internal organization, give information about what the primitive condition of molluscs may have been without being themselves primitive. A Late Cambrian-Early Ordovician origin from a large aculiferan form with a developed mantle groove and posterior mantle cavity is postulated.

The cladogram calls for certain characters to have evolved more than once: gills, single or paired digestive gland separate from the stomach, gastric shield and/or style sac (present in Monoplacophora and other Conchifera and in the derived aplacophoran family Chaetodermatidae, Scheltema 1978), and pericalymma larva (protobranch bivalves, Aplacophora). Other molluscan larval types have not been considered. Selection seems to have worked on both larval stages and adults in the Mollusca, and the larvae do not clarify evolutionary pathways within the phylum. The arguments presented here are incomplete but provide an outline for further development. Tests of the cladogram lie in biochemical analyses and the embryology of Monoplacophora and Aplacophora.

With shell and spicules considered as synapomorphies for the Conchifera and Aculifera, respectively, the following classification of extant Mollusca emerges:

## Phylum Mollusca

### Subphylum Conchifera

#### Class Monoplacophora

#### Class Bivalvia

#### Class Gastropoda

Class Scaphopoda

Class Cephalopoda

Subphylum Aculifera

Class Polyplacophora

Class Aplacophora

Subclass Neomeniomorpha

Subclass Chaetodermomorpha

This arrangement is similar to that already proposed in the last century (Table 1), but the rationale behind the latter was based on shared plesiomorphies of the nervous system and no knowledge of Monoplacophora. It is curious that a classification based on presumed shared apomorphies and a hypothetical metameric ancestor should be much the same.

## BIOGEOGRAPHY AND THE DEEP-SEA FAUNA

Biogeography is the study of species distributions in space and the processes, both contemporary and historical, that have determined distributional patterns. The deep sea is defined here as the sea floor that lies at depths greater than 200 m, an enormous space that accounts for 92.4% of the ocean bottom (Sverdrup et al. 1942, p. 19). It has unique characteristics and history reflected in its fauna. A summary of the deep sea and its molluscan fauna, including the physical, chemical, and organic description of the environment, is given in Allen (1983). Monniot and Monniot (1978) have described the systematics, natural history, and biogeography of deep-sea tunicates in the well-sampled North and South Atlantic Oceans. The Galathea Reports often cover broad biogeographic topics (e.g. Madsen 1961; Hansen 1975). Gage and Tyler (1991) review the biogeography of all animal groups and are a source for references.

Species of Aplacophora are nearly always present in fine-sieved deep-sea benthic samples from all depths but are seldom a numerically dominant part of the fauna. Aplacophorans are a small taxon with less than 300 published species and perhaps 400 or more species still to be described. The class is ubiquitous in the deep sea and some genera are very widespread (Scheltema 1990) and consequently a few genera and species provide much biogeographic information.

The Aplacophora are congruent in their history, distribution, and adaptation with many of the general biogeographic patterns characteristic of other deep-sea taxa. Allen (1983) believes that the deep-sea molluscan fauna is represented primarily by ancient groups. The three deep-sea "primitive" molluscan classes — Aplacophora, which probably evolved in the Upper Cambrian or Ordovician, the Monoplacophora, which date from at least the mid-Cambrian (Runnegar and Pojeta 1985), and the Polyplacophora, represented by the genus *Lepidopleurus* with roots in the Carboniferous (Moore 1960) — are among these ancient groups.

The small size of aplacophorans and other deep-sea taxa relative to the availability of food is discussed above in the section on Phylogeny. The subject of nutrition and feeding in the deep sea is reviewed by Gage and Tyler (1991).

There are only a few regions where aplacophoran collections have been made from both the continental shelf and the adjacent slope and abyss on which comparisons of diversity, abundance, vertical range and geographic distribution can be made. Recent collections off southeast Australia are notable exceptions (Scheltema 1989, 1990). If all published species of neomenioids (Appendix A) are tallied by depth, the largest number, 87 species, is found on the continental shelf from 0 to 200 m, followed by depths between 200 and 500 m with 64 species and by 47 species between 500 and 1,000 m. Below 1,000 m species numbers drop off rapidly. However, most published species are based on only one or a few specimens, so that neither their vertical nor horizontal distribution is known, and the numbers seem mostly to reflect collecting effort rather than actual distributions. With adequate sampling as off southeast Australia, the high diversity of the aplacophoran slope fauna becomes evident. A single epibenthic sled sample from 400 m contained 20 species and more than 500 specimens of neomenioids. In contrast, the greatest diversity in epibenthic sled subsamples from the continental shelf in the same region was only 3 or 4 species and 10 to 30 specimens. The ten-fold difference cannot be attributed to sample size alone but reflects the fact that the Aplacophora are primarily a deep-sea taxon of the upper continental slope, that is, between the edge of the continental shelf and 3,000 m.

Other invertebrate taxa are also known to be more diverse in the deep sea than in the littoral and sublittoral, such as the protobranch bivalves (Allen 1983) and asellote isopods (Hessler et al. 1979). The question arises as to where the deep-sea fauna originated. Initial evidence from disjunct Mediterranean, western Atlantic, and western Pacific families and genera indicates that aplacophorans already had evolved on the upper slope before the closure of the Tethyan Sea and they apparently have migrated up the slope onto the continental shelf (Scheltema 1990). Such a process of upward migration may have broad implications for other deep-sea taxa. However, some groups such as the asellotes are phylogenetically more derived in the deep sea than in shallow water (Hessler et al. 1979), and the same tunicate genera and families occur both sublittorally and in the deep-sea (Monniot and Monniot 1978). In both asellotes and tunicates a shallow-water origin is indicated. For asellotes, a subsequent upward migration into high-latitude environments from the deep sea has occurred (Hessler et al. 1979). Some aplacophoran species have wide geographic distributions within the Atlantic or Pacific Ocean, and, as in protobranch bivalves, the magnitude of their vertical (depth) distribution is correlated with the number of basins in which they are found (Scheltema 1985). Three Atlantic species of Prochaetodermatidae with a vertical range greater than 1,500 m are found in four or more basins and are amphi-Atlantic; of these one is abyssal and two are slope species. A fourth species with a vertical range of 1200 m occurs in two basins, and a fifth abyssal species with a vertical range of 500 m is restricted to a single basin (Scheltema 1985). As in many deep-sea tunicates (Monniot and Monniot 1978) the amphi-Atlantic species extend from the West European Basin south to the Namibia Basin off southwest Africa in the eastern Atlantic but are restricted to the North American Basin in the western Atlantic (Scheltema 1985). Both the aplacophoran and

tunicate faunas are more diverse in the eastern than in the western North Atlantic (Scheltema 1985b, Monniot and Monniot 1978).

No species has yet been recorded from both the Atlantic and Pacific although circum-Antarctic species (Salvini-Plawen 1978b) may eventually be found to extend northward into both. Essentially nothing is known of the Indian Ocean aplacophoran fauna.

The aplacophoran hydrothermal vent fauna in both the eastern and western Pacific is dominated by the neomenioid genus *Helicoradomenia* (Scheltema and Kuzirian 1991). The genus is comprised of 8 or 9 species; the radulae and copulatory spicules of 7 are shown in Figure 9. Like many other vent taxa (Jones 1985) *Helicoradomenia* is known only from vent sites.

The aplacophoran fauna of the deep coastal eastern North Pacific is currently under study. This area is dominated by the genus *Chaetoderma* with 15 or more species, many of them endemic. Dominance by the genus *Chaetoderma* is unknown from any other region except probably the Sea of Japan (Ivanov 1984). There is a marked difference in the fauna north and south of the latitude of Pt. Conception, California. Some species to the north of Pt. Conception extend to southern Alaska and one species apparently crosses the Pacific to the Sea of Japan (Scheltema et al. 1991).

Certain aspects of aplacophoran distributions and biology are unique among the deep-sea fauna. For instance, the only species described from hadal depths greater than 6,000 m, *Chevroderma whitlatchi*, is not restricted to trenches but occurs in the central and eastern North Pacific at depths as shallow as 2,800 m (Scheltema 1985). Its occurrence in the Aleutian Trench at 7,200 m could be due to colonization by slumping, that is the animals were carried downward from the rim of the Trench with the slumping sediment. Second, the rapid growth to maturity of *Prochaetoderma yongei* discussed above (Phylogeny; Scheltema 1987) does not fit the usual view that life processes in the deep sea are slow (Allen 1983; but see Gage and Tyler [1911] for other examples of rapid growth).

Vast areas of the oceanic benthos remain to be sampled, particularly the Pacific and Indian oceans, and many aplacophoran collections still await description. Further knowledge on the biogeography of the Aplacophora will give insights into the evolution of the deep-sea fauna.

## ECOLOGY

Little is known about the ecology of Aplacophora, although they are common in the deep sea and in some localities an aplacophoran species may be one of the numerically dominant forms (*Chevroderma whitlatchi*, Scheltema 1985; *Prochaetoderma yongei*, *Spathoderma clenchi*, Maciolek et al. 1986). Diets have been determined from gut contents or, in the case of some neomenioids, attachment to prey species of Cnidaria, but the actual mode of feeding has not been observed directly. Preserved neomenioids sometimes have an everted pharynx and seem to be

sucking cnidarian tissue, but the role of the radula is unknown. The only radulae with worn distal teeth are found in the omnivorous Prochaetodermatidae (Scheltema 1981). In one specimen a foraminifera with holes presumably rasped in its shell was found held between the jaws within a greatly expanded pharynx. *Chaetoderma nitidulum* is carnivorous on foraminifera and must be removed from mud samples collected for living forams (Bengt Christiansen, personal communication). Species of *Helicoradomenia* from hydrothermal vents have no nematocysts from Cnidaria in the gut (Scheltema and Kuzirian 1991) and their diet is suspected to be sulfur-fixing bacteria, the primary producer at the vents.

Colonization experiments in combination with large epibenthic sled samples have provided some meager, albeit interesting, data on the life history of a single species, *Prochaetoderma yongei* (see section on Phylogeny above; Scheltema 1987). Other ecological data remain fragmentary and have not been published except as scattered accounts accompanying species descriptions. Aplacophora are mostly cold-water, probably stenotopic organisms but there are exceptions. One of the most interesting is the large shallow-water, tropical neomenioid genus *Epimenia* which grows to 30 cm (see Scheltema 1989). It has provided the only aplacophoran material for experimental physiology (Baba 1940b). Species of the chaetoderm family Scutopidae (*Scutopus*, *Psilodens*) can apparently exist in physically stressed environments. A species of *Psilodens* has been collected from 60 m or less in the Gulf of Panama, where annual upwelling lowers the temperature at 38 m by 10°C and raises salinity by 2.50‰ (Smayda 1966). A species of *Scutopus* from 20 m in the Bay of Bengal off Madras, India, is probably living in an area affected by lowered salinities during the annual monsoons (Jacob and Rangarajan 1959). In central California an oxygen minimum zone (<0.5 ml/l O<sub>2</sub>) impinges on the coast between about 500 and 1000 m (Thompson et al. 1985). Just below lies a dysaerobic zone (<1.0 ml/l O<sub>2</sub>) where two species of Scutopidae are found both of which continue downslope below the dysaerobic zone to 3,000 m.

*Chaetoderma nitidulum* is a stenotopic amphi-Atlantic species (Scheltema 1973). In Cape Cod Bay, Massachusetts, the species is restricted to temperatures below 10°C and to sediments with not more than 20% clay. Presumably because of pollution it has now disappeared from Oslo Harbor, where it was common a hundred years ago as evidenced by specimens deposited in the Zoological Museum of the University of Oslo. *Chaetoderma argenteum*, perhaps as a response to El Niño events, has disappeared from Monterey Bay, California, where numerous specimens were collected a hundred years ago, but it still remains in deeper water offshore (Scheltema et al. 1991).

## FUTURE DIRECTIONS FOR RESEARCH

Ecological, physiological, and developmental studies on Aplacophora are difficult but not impossible (e.g. Baba 1940c, Scheltema 1987, Buckland-Nicks and Chia 1989). Cold-water chaetoderms with carnivory on foraminifera are easy to maintain at cold temperatures in the laboratory in coarsely sieved mud containing their food (unpublished). Neomenioids are apparently more difficult to keep (Baba 1940c).

The difficulties of making proper identifications as well as collecting has been a hindrance to experimental work and observations on living aplacophorans. Thus the descriptions of new species continue. As species become known, insights will be gained about deep-sea biogeography, ecology, and animal diversity.

Where there is access to living material close to shore facilities, such as in the fjords of Norway, much can be discovered about locomotion (continuing the work of Salvini-Plawen 1968a, d), gametogenesis (continuing the work of Buckland-Nicks and Chia 1989), development (continuing the work of Baba 1938, 1940c and Thompson 1960), reproduction, feeding, physiological rates, digestion (continuing the work of Baba 1940b), sensory responses (following the TEM studies of Haszprunar 1986, 1987), taxes, animal-sediment relationships — in a word, all the activities of a living organism.

Histologic examination of new species constantly brings to light new information. For instance, the existence of spermatophores has been documented for the first time (Scheltema et al. *in press b* Fig. 23B). From histology, parasites become evident (e.g., Scheltema et al. *in press b* Fig. 11c) and their occurrence can be related to energetics of the deep sea. Fine structure analysis by TEM provides information on both animal activity and phylogeny. As discussions of molluscan phylogeny continue, the Aplacophora will be critical to these debates.

With increasing pressure to dump garbage and toxic and radioactive wastes in the deep sea, there needs to be increased knowledge of the ecology of the deep-sea benthos. Aplacophora as a small taxon with a predictable presence may provide key species to understanding the effects of dumping.

Systematic studies of organisms are opening the door to the broadest vistas of interactions and interdependence between life and our planet. The Aplacophora have a small but important place in the grand scheme.

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## REFERENCES

- Allen, J. A. 1983. The ecology of deep-sea molluscs. Pp. 29-75. In: W. D. Russell-Hunter (ed.) The Mollusca. Vol. 6 Ecology. Academic Press, Orlando, FL.
- Baba, K. 1938. The later development of a solenogastre, *Epimenia verrucosa* (Nierstrasz). J. Dept. Agricul., Kyusyu Imperial Univ. 6:21-40.
- Baba, K. 1939. Preliminary note on *Epimenia verrucosa* (Nierstrasz), a solenogastre species from Amakusa, Japan. Venus (Tokyo) 9:35-42. [English summary]
- Baba, K. 1940a. *Epimenia ohshimai* a new solenogastre species from Amakusa, Japan. Venus (Tokyo) 10:91-96. [English summary]
- Baba, K. 1940b. The mechanisms of absorption and excretion in a solenogastre, *Epimenia verrucosa* (Nierstrasz), studied by means of injection methods. J. Dept. Agricul., Kyusyu Imperial Univ. 6:119-166.
- Baba, K. 1940c. The early development of a solenogastre, *Epimenia verrucosa* (Nierstr.). Annot. zool. jap. 19:107-113.
- Baba, K. 1975. *Neomenia yamamotoi* spec. nov., a gigantic solenogaster (Mollusca: Class Solenogastres, Family Neomeniidae), occurring in the north-eastern part of Japan. Publ. Seto Mar. Biol. Lab. 22(5):277-284.
- Baird, W. 1868. Monograph of the species of worms belonging to the subclass Gephyrea; with a notice of such species as are contained in the collection of the British Museum. Proc. Zool. Soc. London (1868):76-114, pl. 9-11.
- Beedham, G. E. and E. R. Trueman. 1968. The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. J. Zool. 154:443-451.
- Belyaev, G. M. 1989. Glubokovodnii Okeanicheskii Zheloba i ikh fauna. Moscow "Nauka".
- Boettger, C. R. 1956. Beiträge zur Systematik der Urmollusken (Amphineura). Verh. dtsch. Zool. Ges., Zool. Anz. Suppl. 19, 1955:223-256.
- Boss, K. J. 1982. Mollusca. Pp. 945-1166. In: S. P. Parker (ed.), Synopsis and classification of living organisms Vol. 1. McGraw Hill, New York.
- Bouchet, P. and A. Warén. 1979. The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. Sarsia 64:211-243.

- Buckland-Nicks, J. and F.-S. Chia. 1989. Spermiogenesis in *Chaetoderma* sp. (Aplacophora). J. Exp. Zool. 252:308-317.
- Butterfield, N. J. 1990. A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. Paleobiology 16:287-303.
- Conway Morris, S. 1985. The Middle Cambrian metazoan *Wiwaxia carrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. Phil. Trans. Roy. Soc. London, B, 307:507-586.
- Derjugin, K. M. 1915. [Fauna of the Kola gulf and its life conditions.]. Mem. Acad. Imp. Sci. Petrograd (ser. 8), 34(1):1-929, t. 1-14 [pp. 499-501 Solenogastres]. [In Russian]
- Derjugin, K. M. 1928. Fauna des Weissen Meeres und ihre Existenzbedingungen. Explorations des Mers d'U.R.S.S., fasc. 7-8, 1-511 [pp. 294-295, Solenogastres].
- Diesing, K. M. 1859. Revision der Rhyngodeen. Sitz. K. Akad. Wiss., Wien, Math.-Nat. Classe 37:719-782, pl. 1-3.
- Eyster, L. S. and M. P. Morse. 1984. Early shell formation during molluscan embryogenesis, with new studies on the surf clam, *Spisula solidissima*. Amer. Zool. 24:871-882.
- Field, K. G., G. J. Olsen, D. J. Lane, S. J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace and R. A. Raff. 1988. Molecular phylogeny of the animal kingdom. Science 239:748-753.
- Gage, J. D. and P. A. Tyler. 1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, U.K. xvi+503 pp.
- Gegenbaur, C. 1878. Grundriss der vergleichenden Anatomie. 2<sup>nd</sup> ed. Leipzig: Wilhelm Engelmann.
- Gould, S. J. 1977. Ontogeny and Phlogeny. Harvard Univ. Press, Cambridge, MA and London. xiv+501 pp.
- Graff, L. von. 1876. Anatomie des *Chaetoderma nitidulum*. Z. wiss. Zool. 26:166-192, pl. 11-13.
- Haas, W. 1977. Observations of the shell and mantle of the Placophora. In: N. Watabe, K. M. Wilbur (eds.), The mechanisms of mineralization in invertebrates and plants. Bell W. Baruch Library in Marine Science 5:389-402.

- Haas, W. 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia* 21:403-418.
- Hammarsten, O. D. and J. Runnström. 1925. Zur Embryologie von *Acanthochiton discrepans* Brown. *Zool. Jb., Anat.* 47:261-318.
- Hansen, B. 1975. Systematics and biology of the deep-sea holothurians. *Galathea Report* 13: 262 pp., 14 plates.
- Hansen, G. A. 1877. Anatomisk beskrivelse af *Chaetoderma nitidulum*, Lovén. *Nyt mag. Natur.* 22:354-377, pl. 1-5.
- Haszprunar, G. 1986. Fein morphologische Untersuchungen an Sinnes strukturen ursprünglicher Solenogastres (Mollusca). *Zool. Anz.* 217:345-362.
- Haszprunar, G. 1987. The fine morphology of the osphradial sense organs of the Mollusca. IV. Caudofoveata and Solenogastres. *Philos. Trans. Roy. Soc. London B* 315:63-73.
- Heath, H. 1904. The nervous system and subradular organ in two genera of solenogastres. *Zool. Jb., Anat.* 20:399-408, pl. 27.
- Heath, H. 1905. The morphology of a Solenogastre. *Zool. Jb., Anat.* 31:703-734, pl. 42-43.
- Heath, H. 1911. The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific...by the "Albatross"... . *Mem. Mus. Comp. Zool.* 45(1):1-179 + 40 plates.
- Heath, H. 1912. *Spengelomenia*, a new genus of solenogastres. *Zool. Jb., Suppl.* 15(1):465-478.
- Heath, H. 1918. Solenogastres from the Eastern Coast of North America. *Mem. Mus. Comp. Zool.* 45(2):185-263, pl. 1-14.
- Hessler, R. R. and P. A. Jumars. 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.* 21:185-209.
- Hessler, R. R. and H. L. Sanders. 1967. Faunal diversity in the deep sea. *Deep-Sea Res.* 14:65-78.
- Hessler, R. R., G. D. Wilson and D. Thistle. 1979. The deep-sea isopods: a biogeographic and phylogenetic overview. *Sarsia* 64:67-75.

- Hoffman, S. 1949. Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. Zool. Bidr. Uppsala 27:293-427.
- Hoffmann, H. 1929-30. Aplacophora. Bronn's Kl. Ordn. Tier. Band III, Abt. I:1-134, 383-453.
- Hubrecht, A. A. W. 1888. *Dondersia festiva* gen. et spec. nov. Donders Feestbundel. Nederl. Tijdschr. van Geneesk., pp. 324-339, pl. 8-9.
- Hulings, N. C. and J. S. Gray. 1971. A manual for the study of meiofauna. Smithsonian Contr. Zool. 78:xi+84 pp.
- Hyman, L. H. 1967. The Invertebrates. Vol. VI. Mollusca I. McGraw Hill, New York. vii+792.
- Ihering, H. v. 1877. Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken. Leipzig.
- Ivanov, D. L. 1981. [*Caudofoveatus tetradens* gen. et sp. n. and diagnosis of taxa in the subclass Caudofoveata (Mollusca, Aplacophora).] Zool. Zhur. (Akad. Nauk SSSR) 60:18-28. [In Russian]
- Ivanov, D. L. 1984. [Caudofoveats (Mollusca, Caudofoveata) in Peter the Great Bay.] Pp. 28-41. In: A. I. Kafanov (ed.), [Hydrobiological research of bays and inlets of Primorye.] Far East Science Center, USSR Acad. Sci. Vladivostok. [In Russian]
- Ivanov, D. L. 1986. [New forms of Caudofoveata in the Chukotskoya (Chukchi) Sea.] Arch. Zool. Mus. Moscow 24:83-95, 4 figs.
- Ivanov, D. L. 1987. Class Aplacophora Ihering, 1876. Pp. 28-35, figs. 1-6. In: A. O. Scarlato (ed.), [Mollusca of the Beloge (White) Sea.] Zool. Inst. Akad. Nauk SSSR Leningrad.
- Ivanov, D. L. 1990. [Radula in the class of shell-less molluscs (Aplacophora).] In: D. L. Ivanov (ed.), [Evolutionary morphology of molluscs.] Arch. Zool. Mus. Moscow 28:198, 213-222. [In Russian]
- Jacob, J. and K. Rangarajan. 1959. Seasonal cycles of hydrological events in Vellar Estuary. Proc. 1<sup>st</sup> All-India Congress of Zoology, pp. 329-350. Calcutta.
- Jones, M. L. (ed.) 1985. Hydrothermal vents of the Eastern Pacific: an overview. Bull. Biol. Soc. Washington 6:1-545.

- Kaiser, P. 1976. *Neomenia herwigi*, sp. n., ein bemerkenswerter Vertreter der Solenogastren (Mollusca, Aculifera) aus Argentinischen Schelfgewässern. Mitt. Hamburg Zool. Mus. Inst. 73:57-63.
- Keferstein, W. 1865. Beiträgen zur anatomischen und systematischen Kenntniss der Sipunculiden. Z. wiss. Zool. 15:404-449.
- Knipowitsch, N. 1896. Eine zoologische Exkursion im nordwestlichen Teile des Weissen Meeres im Sommer 1895. Ann. Mus. Zool. Acad. Imp. Sci. St. Petersburg 1:278-326.
- Kniprath, E. 1980. Ontogenetic plate and plate field development in two chitons, *Middendorffia* [= *Lepidochitona*] and *Ischnochiton*. Wilh. Roux's Arch. dev. Biol. 189:97-106.
- Knudsen, J. 1949. Amphineura. Zool. Iceland 4(59):1-11.
- Koren, J. and D. C. Danielssen. 1877. Beskrivelse over nye arter, henhørende til slægten Solenopus, samt vogle oplysninger om dens organisation. Arch. Math. Naturvidenskab 2:120-128.
- Kowalevsky, A. 1901. Sur le genre Chaetoderma. Arch. Zool. exp. (ser. 3) 9:261-284, pl. 10-12.
- Kowalevsky, A. and A. F. Marion. 1882. Études sur les Neomenia. Zool. Anz. 5:61-64.
- Kowalevsky, A. and A. F. Marion. 1887. Contributions à l'histoire des Solenogastres ou Aplacophores. Ann. Mus. d'Hist. Nat. Marseille. Zool. 3(1):1-77, pl. 1-7.
- Lankester, E. R. 1877. Notes on embryology and classification of the animal kingdom. Quart. J. Microsc. Soc. (n.s.) 17:448.
- Leloup, E. 1950. Solenogastres provenant des campagnes du Prince Albert 1<sup>er</sup> de Monaco. Rés. Camp. Sci. Fasc. 110, 38 pp. + 8 pl.
- Lemche, H. and K. G. Wingstrand. 1959. The anatomy of *Neopilina galathea* Lemche, 1957 (Mollusca Tryblidiacea). Galathea Rept. 3:9-71, 56 pl.
- Lovén, S. 1844. *Chaetoderma*, ett nytt maskslägte n. g. Ofv. K. vet.-akad. Förh. 1(5):116, pl. 2.
- Lummel, L. E. A. van. 1930. Untersuchungen über einige Solenogastren. Z. Morph. Oekol. 18:347-383.

- Maciolek, N., J. F. Grassle, B. Hecker, P. D. Boehm, B. Brown, B. Dade, W. G. Steinauer, E. Baptiste, R. E. Ruff and R. Petrecca. 1986. Study of biological processes on the U.S. Mid-Atlantic Slope and Rise. OCS Study MMS 86-0000, Final Draft Rept., U.S. Dept. Interior, Minerals Management Service.
- Madsen, F. J. 1961. The Porcellanasteridae: a monographic revision of an abyssal group of sea-stars. *Galathea Rept.* 4:33-174, 13 pl.
- Monniot, C. and F. Monniot. 1978. Recent work on the deep-sea tunicates. *Oceanogr. Mar. Biol. Ann. Rev.* 16:181-228.
- Moore, R. C. (ed.) 1960. Treatise on invertebrate paleontology. Part I. Mollusca 1. Geological Society of America, Inc. and University of Kansas Press, Lawrence, Kansas.
- Morse, M. P. 1979. *Meiomenia swedmarki* gen. et sp. n., a new interstitial solenogaster from Washington, USA. *Zool. Scr.* 8:249-253, 11 figs.
- Morse, M. P. and A. H. Scheltema. 1988. Aplacophora. Pp. 447-450. In: R. P. Higgins and H. Thiel (eds.). Introduction to the Study of Meiofauna. Washington, D.C. and London, Smithsonian Institution Press.
- Newman, W. A. 1985. The abyssal hydrothermal vent invertebrate fauna: a glimpse of antiquity? *Biol. Soc. Washington Bull.* 6: 231-242.
- Nierstrasz, H. F. 1902. The solenogastres of the Siboga-Expedition. *Siboga-Expeditie* 47. E. J. Brill, Leyden. 46 pp., 6 pl.
- Nierstrasz, H. F. 1903. Neue Solenogastren. *Zool. Jb., Anat.* 18:359-386, pl. 35-36.
- Nierstrasz, H. F. 1905. *Kruppomonia minima* und die Radula der Solenogastren. *Zool. Jb., Anat.* 21:655-702, pl. 39-41.
- Nierstrasz, H. F. 1908. Mollusca. VII. Solenogastres. *Nat. antarct. Exp. [Discovery]* 4:38-46, 2 pl.
- Ockelmann, K. 1964. An improved detritus-sledge for collecting meiobenthos. *Ophelia* 1:217-222.
- Odhner, N. H. 1921. Norwegian Solenogastres. *Bergens Mus. Aarbok* 1918-1919, N. r. 3:1-86, 6 pl.
- Okuda, S. 1943. The fauna of Akkeshi Bay. XIV. Solenogastre. *Annot. zool. jap.* 22:11-14, text figs.

- Osoria, R. C. and E. Tarifeño. 1976. A new species of aplacophorous mollusk from the Southeastern Pacific Ocean: *Chaetoderma araucanae* spec. nov. (Mollusca: Caudofoveata: Chaetodermatidae). *Veliger* 19:84-89.
- Pelseneer, P. 1901. Les néoméniens de l'expédition antarctique belge et la distribution géographique des Aplacophora. *Bull. Cl. Sci. Acad. Roy. Belg.* 1901:528-534, 1 pl.
- Pelseneer, P. 1906. Mollusca. In: E. R. Lankester (ed.), *A treatise on zoology*. Part 5. Black, London.
- Ponder, W. F. 1970. A new aplacophoran from New Zealand. *J. Malac. Soc. Australia* 2: 47-54, 14 text figs.
- Pruvot, G. 1891. Sur l'organisation de quelques Néoméniens des côtes de France. *Arch. Zool. Exp. Gén.* (ser. 2) 9:699-805, pl. xxv-xxxi.
- Pruvot, G. 1899. Sur deux Néoméniens nouveaux de la Méditerranée. *Arch. Zool. Exp. Gén.* (ser. 3) 7:461-509, pl. 12-14.
- Runnegar, B. and J. Pojeta, Jr. 1985. Origin and diversification of the Mollusca. Pp. 1-57. In: E. R. Trueman and M. R. Clarke (eds.), *The Mollusca*, Vol. 10. Evolution. Academic Press, Orlando.
- Salvini-Plawen, L. v. 1967. Neue Scandinavische Aplacophora (Mollusca, Aculifera). *Sarsia* 27:1-63, 63 figs.
- Salvini-Plawen, L. v. 1968a. Über Lebendbeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia* 31:105-126.
- Salvini-Plawen, L. v. 1968b. Beiträge zur Systematik der Niederen Mollusken. *Proc. Symp. Mollusca. Mar. Biol. Assoc. India* 1:248-256.
- Salvini-Plawen, L. v. 1968c. Neue Formen im marinen Mesopsammon: Kamptozoa und Aculifera (nebst der für Adria neuen Sandfauna). *Ann. Naturhist. Mus. Wien* 72:231-272.
- Salvini-Plawen, L. V. 1968d. Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Sarsia* 31:131-142.
- Salvini-Plawen, L. v. 1969. Faunistische Studien am Roten Meer im Winter 1961/62: V. Caudofoveata und Solenogastres (Mollusca, Aculifera). *Zool. Jb., Syst.* 96:52-68.
- Salvini-Plawen, L. v. 1970. Die norwegischen Caudofoveata (Mollusca, Aculifera). *Sarsia* 45:1-16.

- Salvini-Plawen, L. v. 1971. Die nordatlantischen Caudofoveata des Zoologischen Museums zu Kopenhagen (Mollusca, Aculifera). *Steenstrupia* 2:27-34.
- Salvini-Plawen, L. v. 1972a. Die Caudofoveata des Mittelmeeres und das Genus *Scutopus* (Mollusca, Aculifera). Pp. 27-51. In: B. Battaglia (ed.) Fifth European Marine Biology Symposium. Piccin Editore, Padua.
- Salvini-Plawen, L. v. 1972b. Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Z. wiss. Zool.* 184:205-394.
- Salvini-Plawen, L. v. 1975. Mollusca Caudofoveata. Marine Invertebrates of Scandinavia 4. Universitetsforlaget, Oslo, 55 pp.
- Salvini-Plawen, L. v. 1977a. Caudofoveata (Mollusca), Priapulida und apode Holothurien (*Labidoplax*, *Myriotrochus*) bei Banyuls und im Mittelmeer allgeheim. *Vie Mil.* 27 A:55-81.
- Salvini-Plawen, L. v. 1977b. Caudofoveata (Mollusca) des Forschungsprojektes Polymède. *Bull. Mus. nat. Hist. nat. (3<sup>e</sup> sér.)*, no. 447, Zoologie 310:413-421.
- Salvini-Plawen, L. v. 1978a. The species-problem in Caudofoveata (Mollusca). *Zool. Anz.* 200:18-26, figs. 1-10.
- Salvini-Plawen, L. v. 1978b. Antarktische und subantarktische Solenogastres (eine Monographie: 1898-1974). *Zoologica (Stuttgart)* 44:1-315.
- Salvini-Plawen, L. v. 1981. On the origin and evolution of the Mollusca. *Atti Convegni Lincei* 49: 235-293.
- Salvini-Plawen, L. v. 1984. [Comments on *Chaetoderma* and *Crystallophrisson* (Mollusca, Caudofoveata).] *Zool. Zhur.* 63:171-175. [In Russian]
- Salvini-Plawen, L. v. 1985a. New interstitial solenogastres (Mollusca). *Stygologia* 1:101-108.
- Salvini-Plawen, L. v. 1985b. Early evolution and the primitive groups. Pp. 59-150. In: E. R. Trueman and M. R. Clarke (eds.), *The Mollusca*, Vol. 10. Evolution. Academic Press, Inc., Orlando. xx+491 pp.
- Salvini-Plawen, L. v. 1988. Einige Solenogastres (Mollusca) der europäischen Meiofauna. *Ann. Naturhist. Mus. Wien* 90(B):373-385.
- Salvini-Plawen, L. v. and A. Warén. 1972. Skandinavische Caudofoveata (Mollusca): Nachtrag. *Sarsia* 51: 3-5.



- Sanders, H. L. and J. A. Allen. 1973. Studies on deep-sea Protobranchia (Bivalvia); Prologue and the Pristiglomidae. *Bull. Mus. Comp. Zool.* 145:237-262.
- Sars, M. 1869. Fortsatte bemaerkninger over det dyriske livs udbredning i havets dybder. *Forh. Vid.-selsk. Christiana* 1868:246-275.
- Scheltema, A. H. 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Z. Morph. Tiere* 72:361-370.
- Scheltema, A. H. 1973. Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Z. Morph. Tiere* 76:97-107.
- Scheltema, A. H. 1976. Two new species of *Chaetoderma* from off west Africa (Aplacophora, Chaetodermatidae). *J. Moll. Stud.* 42:223-234.
- Scheltema, A. H. 1978. Position of the class Aplacophora in the phylum Mollusca. *Malacologia* 17:99-109.
- Scheltema, A. H. 1985a. The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca: Chaetodermomorpha). *Biol. Bull.* 169:484-529.
- Scheltema, A. H. 1985b. The genus *Prochaetoderma* (Aplacophora, Mollusca): Initial account. Pp. 391-396. In: L. Laubier and Cl. Monniot (eds.), *Peuplements profonds du golfe de Gascogne*. IFREMER (Brest).
- Scheltema, A. H. 1989. Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off southeastern Australia. *Rec. Australian Mus.* 41:43-62.
- Scheltema, A. H. 1990. Aplacophora as a Tethyan slope taxon: evidence from the Pacific. *Bull. Mar. Sci.* 47:50-61.
- Scheltema, A. H., J. Buckland-Nicks and F.-S. Chia. 1991. *Chaetoderma argenteum* Heath, a northeastern Pacific aplacophoran mollusk redescribed (Chaetodermomorpha: Chaetodermatidae). *Veliger* 34:204-213.
- Scheltema, A. H., K. Kerth and A. M. Kuzirian. 1989. The primitive molluscan radula. *Unitas Malacologica* 10<sup>th</sup> International Congress, 27 August-2 September, 1989, Tübingen, Germany. [Abstract]
- Scheltema, A. H. and A. M. Kuzirian. 1991. *Helicoradomenia juani* n.g. n. sp., a Pacific hydrothermal vent Aplacophora (Mollusca, Neomeniomorpha). *Veliger* 34:195-203.

- Scheltema, R. S. and A. H. Scheltema. 1972. Deep-sea studies in America. 1846-1872 - their contribution to the CHALLENGER Expedition. Proc. Roy. Soc. Edinburgh (B) 72 (1971-1972):94-104.
- Schwabl, M. 1955. *Rupertomenia fodiens* nov. gen. nov. sp. eine neue Lepidomeniide von der Sudwestküste Schwedens. Öst. zool. Zeit. 6:90-146, figs. 1-16.
- Schwabl, M. 1963. Solenogaster mollusks from southern California. Pac. Sci. 17(3):261-281.
- Selenka, E. 1885. Report on the Gephyrea collected by H.M.S. Challenger during the years 1873-1876. Rept. Sci. Res. Challenger 13(2):25 pp., 4 pls.
- Simroth, H. 1892-1894. Mollusca: Amphineura und Scaphopoda. Bronn's Kl. Ordn. Tier., Bd. III, Abt. 1:133-233.
- Smayda, T. J. 1966. A quantitative analysis of phytoplankton of the Gulf of Panama. III. Ecological conditions.... Inter-American Tropical Tuna Commission, La Jolla, California, pp. 354-612.
- Soetaert, K. and C. Heip. 1989. The size structure of nematode assemblages along a Mediterranean deep-sea transect. Deep-Sea Res. 36:93-102.
- Spengel, J. W. 1881. Die geruchsorgane und das nervensystem der mollusken. Z. wiss. Zool. 35:333-383, pl. 17-19.
- Stasek, C. R. 1972. The molluscan framework. In: M. Florkin and B. T. Scheer (eds.), Chemical Zoology, VII. Mollusca, pp. 1-44.
- Sverdrup, H. U., M. W. Johnson, and R. H. Fleming. 1942. The oceans -- their physics, chemistry, and general biology. Prentice-Hall, New York. x+1087 pp.
- Thiele, J. 1894. Beiträge zur vergleichenden Anatomie der Amphineuren. I. Über einige Neapeler Solenogastres. Z. wiss. Zool. 58:222-302, pl. 12-16.
- Thiele, J. 1897. Zwei australische Solenogastres. Zool. Anz. 20:398-400.
- Thiele, J. 1900. *Proneomenia thulensis* nov. spec. Fauna Arct. 1:109-116, pl. 5.
- Thiele, J. 1902a. *Proneomenia amboinensis* n. sp. Denkschr. Med. nat. Ges. Jena 8:733-738, pl. 66, figs. 5-9.
- Thiele, J. 1902b. *Proneomenia valdiviae* n. sp. Wiss. Ergebn. dtsch. Tiefsee-Exp. Valdivia 1898-1899, 3:167-174, pl. 23.

- Thiele, J. 1906. *Archaeomenia prisca* n. g., n. sp. Wiss. Ergebn. dtsch. Tiefsee-Exp. Valdivia 1898-1899, 9:315-324, pl. 28.
- Thiele, J. 1911. Die Solenogastres der Russischen Polar-Expedition 1900-1903. Mém. Ac. Sci. St. Pétersb., Ser. 8, 29.
- Thiele, J. 1913a. Antarktische Solenogastren. Dtsch. Südp.-Exp. 14, Zool. 6, Heft 1(2):35-65, pl. 4-8.
- Thiele, J. 1913b. Ein neuer Solenogaster von Spitzbergen. Sitz. Ges. Naturforsch. Freunde Berlin 1913, pp. 160-162, figs. 1, 2.
- Thiele, J. 1925. Solenogastres. Kükenthal and Krumbach (eds.), Handbuch der Zoologie, Bd. 5, Lief. 1:1-14, 7 t-f.
- Thiele, J. 1932. Die Solenogastres des arktischen Gebietes. F. Römer and F. Schaudinn (eds.), Fauna Arctica, Jena, vol. 6, lief. 4: 379-382.
- Thompson, J., H. Mullins, C. Newton and T. Vercoutere. 1985. Alternative biofacies model for dysaerobic communities. Lethaia 18: 167-179.
- Thompson, T. E. 1960. The development of *Neomenia carinata* Tullberg (Mollusca, Aplacophora). Proc. Roy. Soc. London B 153:263-278.
- Thomson, C. W. 1877. Voyage of the "Challenger". The Atlantic. Vol 1, pp. 264-265.
- Tscherkassky, M. 1989. Pedal shield or oral shield in Caudofoveata (Mollusca, Aculifera)? P. 254. In: Unitas Malacologica, Abstracts of 10<sup>th</sup> International Malacological Congress, Tübingen.
- Tullberg, T. 1875. Neomenia, a new genus of invertebrate animals. Bihang K. Svensk. Vet. Akad. Handl. 3(13):12 pp., pl. 1-2.
- Welsch, U. and V. Storch. 1973. Comparative Animal Cytology and Histology. University of Washington Press, Seattle. xiv+343 pp.
- Westheide, W. 1987. Progenesis as a principle in meiofauna evolution. J. Nat. Hist. 21:843-854.
- Wettstein, E. 1904. Anatomie von Cryptoplax. Jen. Z. Naturwiss. 38.
- Willemoes-Suhm, R. v. 1876. Briefe von der Challenger-Expedition. IV. Z. wiss. Zool. 26:LIV [sic].

Wingstrand, K. G. 1985. On the anatomy and relationships of Recent Monoplacophora. *Galathea Rept.* 16:7-94, 12 pl.

Wirén, A. 1892a. Studien über die Solenogastres. I. Monographie des *Chaetoderma nitidulum* Lovén. K. Svensk. Vet. Akad. Handl. 24(12):1-66.

Wirén, A. 1892b. Studien über die Solenogastres. II. *Chaetoderma productum*, *Neomenia*, *Proneomenia acuminata*. K. Svensk. Vet. Akad. Handl. 25(6):1-100.

## **APPENDICES**



(\*) = single specimen, original description

## Appendix A. Named Genera and Species of Neomeniomorpha

### *Acanthomenia* Thiele 1913

*A. gaussiana* Thiele 1913 (\*) Davis Sea, Antarctica

### *Aesthoherpia* Salv.-Pl. 1985

*A. glandulosa* Salv.-Pl. 1985 (type) off Bergen, Norway; Mediterranean

*A. gonoconota* Salv.-Pl. 1988 Norwegian Sea

### *Alexandromenia* Heath 1911

*A. acuminata* Salv.-Pl. 1978 Scotia Sea, Antarctic

*A. agassizi* Heath 1911 (type) Revillagigedo Ids. off Mexico

*A. antarctica* Salv.-Pl. 1978 (\*) Bransfield Str., Antarctic

*A. crassa* Odhner 1921 (\*) Hjelte Fjord, Norway

*A. grimaldii* Leloup 1946 (\*) Azores

*A. latosoleata* Salv.-Pl. 1978 (\*) So. Pacific 55° S. long.

*A. valida* Heath 1911 off So. California

### *Amphimania* Thiele 1889

*A. neapolitana* Thiele 1889 (\*) Naples

### *Anamania* Nierstrasz 1908

*Strophomenia agassizi* Heath 1918 off Nantucket, w. Atlantic

*Proneomenia amboinensis* Thiele 1902 (type) Banda Sea (Amboina)

*Solenopus borealis* Kor. and Dan. 1877 Norway

*Strophomenia farcimen* Heath 1911 Japan, so. of Honshu

*Neomenia gorgonophila* Kowalevsky 1881 ?Mediterranean, Azores

*A. heathi* Leloup 1947 syn. *A. gorgonophila* Kow. 1881

*Strophomenia spinosa* Heath 1911 Japan, so. of Honshu

*Strophomenia triangularis* Heath 1911 Japan, so. of Honshu

### *Archaeomenia* Thiele 1906

*A. prisca* Thiele 1906 Indian Ocean, Agulhas Bank

### *Birasoherpia* Salv.-Pl. 1978

*B. trisialota* Salv.-Pl. 1978 (\*) S.E. Atlantic 33°S, 16°E

### *Biserramenia* Salv.-Pl. 1968

*B. psammobionta* Salv.-Pl. 1968 Adriatic

### *Cyclomenia* Nierstrasz 1902

*C. holosericea* Nierstrasz 1902 (\*) w. of Timor

*Dinomenia* Nierstrasz 1902*D. hubrechtii* Nierstrasz 1902 E. Indian archipelago*Dondersia* Hubrecht 1888*D. annulata* Nierstrasz 1902 (\*) Bay of Bima (n. Sumbawa)*D. californica* Heath 1911 (\*) off San Diego*D. cnidevorans* Salv.-Pl. 1978 (\*) Ross Sea, Antarctic*D. festiva* Hubrecht 1888 (type) Gulf of Naples*D. indica* Stork 1941 (\*) Bay of Bima, Sumbawa [= ?*D. annulata*]*D. laminata* Salv.-Pl. 1978 (\*) Graham Land, Antarctic*D. stylastericola* Salv.-Pl. 1978 (\*) S. Shetlands [juv.]*Dorymenia* Heath 1911*D. acuta* Heath 1911 (type) off So. California*D. acutidentata* Salv.-Pl. 1978 Bransfield Strs., Antarctic*Proneomenia antarctica* Thiele 1913 (?) Davis Sea, Antarctic*D. cristata* Salv.-Pl. 1978 Bransfield Str., Antarctic*Proneomenia discoveryi* Nierstrasz 1908 Ross Sea, Antarctic*D. harpagata* Salv.-Pl. 1978 (\*) S.E. Pacific (54°S, 159°E)*D. hoffmani* Salv.-Pl. 1978 Weddell Sea, Antarctic*D. interposita* Salv.-Pl. 1978 (\*) Tierra del Fuego*Proneomenia longa* Nierstrasz 1902 E. Indian Arch.*D. longa* var. *nierstraszi* Salv.-Pl. 1967 [*nomen nudum*]*D. paucidentata* Salv.-Pl. 1978 Graham Land, Antarctic*D. peroneopsis* Heath 1918 (\*) So. of Martha's Vineyard, Massachusetts*D. profunda* Salv.-Pl. 1978 Amundsen Sea, Antarctic*Proneomenia quincarinata* Ponder 1970 off Chatham Is., N.Z.*Solenopus sarsii* Kor. & Dan. 1877 Oslofjord, Norway*D. singularidentata* Salv.-Pl. 1978 (\*) Bransfield Str., Antarctic*D. tetradoryata* Salv.-Pl. 1978 (2 fragments) Ross Sea, Antarctic*Proneomenia tricarinata* Thiele 1913 Davis Sea, Antarctic*D. usarpi* Salv.-Pl. 1978 Ross Sea, S. Orkney, Antarctic*Proneomenia vagans* Kow. & Mar. 1887 Naples*Proneomenia weberi* Nierstrasz 1902 E. Indian Archipelago*Drepanomenia* Heath 1911*Solenopus incrustata* Kor. & Dan. 1877 Finmark*D. perticata* Salv.-Pl. 1978 (\*) Ross Sea, Antarctic*D. tenuitecta* Salv.-Pl. 1972 [*nomen nudum*]*Neomenia vampyrella* Heath 1905 (type) (\*) off Oahu*Driomenia* Heath 1911*D. pacifica* Heath 1911 Osezaki, Misaki, Japan*Echinomenia* Simroth 1893 syn. *Nematomenia* Simroth 1893



*Eleutheromenia* Salv.-Pl. 1967*Paramenia sierra* Pruvot 1890 (\*) off Spanish coast*Entonomenia* Leloup 1948 syn. *Rhopalomenia* Simroth 1893*Epimenia* Nierstrasz 1908*Proneomenia australis* Thiele 1897 (type) (\*) n.w. coast Australia*E. ohshimai* Baba 1940 Amakusa, Japan*Dinomenia verrucosa* Nierstrasz 1902 E. Indian Arch.*E. vixinsignis* Salv.-Pl. 1978 (\*) Ross Sea, Antarctic*Forcepimenia* Salv.-Pl. 1969*F. protecta* Salv.-Pl. 1969 (\*) Red Sea*Genitoconia* Salv.-Pl. 1967*G. atriolonga* Salv.-Pl. 1967 Norway*G. rosea* Salv.-Pl. 1967 (type) Norway*Gephyroherpia* Salv.-Pl. 1978*G. antarctica* Salv.-Pl. 1978 Ross Sea, Antarctic*Gymnomenia* Odhner 1921*G. pellucida* Odhner 1921 Hardangerfjord, Norway*Gymnomenia* sp. (Scheltema 1981) E. Atlantic*Halomenia* Heath 1911*H. gravida* Heath 1911 Kurile Is.*Harpagoherpia* Salv.-Pl. 1978*H. tenuisoleata* Salv.-Pl. 1978 S. Chile (52°S)*Heathia* Thiele 1913*Ichthyomenia porosa* Heath 1911 off San Diego*Heathimenia* Salv.-Pl. 1967*Neomenia verrilli* Heath 1918 Gulf of St. Lawrence*Helicoradomenia* Scheltema & Kuzirian 1991*H. juani* Schelt. & Kuz. 1991 (type) San Juan Ridge (NE. Pacific)*Hemimenia* Nierstrasz 1902*H. dorsosulcata* Salv.-Pl. 1978 S. Pacific (55°S, 130°W)*H. intermedia* Nierstrasz 1902 (type) E. Indian Arch.*Herpomenia* Heath 1911 syn. *Nematomenia* Simroth 1893

*Heteroherpia* Salv.-Pl. 1978*H. procera* Salv.-Pl. 1978 (\* plus fragments) off Cape Town*Hypomenia* Lummel 1930*H. nierstraszi* Lummel 1930 (\*) Gulf of Naples*Ichthyomenia* Pilsbry 1898*Dondersia* (= *Ismenia*) *ichthyodes* Pruvot 1890 (\*) off Banyuls*Imeroherpia* Salv.-Pl. 1978*I. quadridens* Salv.-Pl. 1978 off Cape Town*Ismenia* Pruvot 1891 syn. *Ichthyomenia* Pilsbry 1898*Kruppomenia* Nierstrasz 1903*K. borealis* Odhner 1921 Norway*K. minima* Nierstrasz 1903 (type) off Naples*Labidoherpia* Salv.-Pl. 1978*Pruvotina spinosa* Thiele 1913 (\*) Davis Sea, Antarctic*Lepidomenia* Kowalevsky in Brock 1883 [awaiting decision by ICZN]*L. harpagata* Salv.-Pl. 1978 (\*) S. Georgia, Antarctic*L. hystrix* Mar. & Kow. in Fischer 1885 (type) (\*) Gulf of Marseille*Lituiherpia* Salv.-Pl. 1978*L. spermathecata* Salv.-Pl. 1978 Tierra del Fuego*Lophomenia* Heath 1911*L. spiralis* Heath 1911 nr. Niihau Is., Hawaii*Lyratoherpia* Salv.-Pl. 1978*L. bracteata* Salv.-Pl. 1978 (\*) So. Sandwich Is., Antarctic [juv.]*L. carinata* Salv.-Pl. 1978 (type) Ross Sea, Antarctic*Macellomenia* Simroth 1893*Paramenia palifera* Pruvot 1890 (\*) Mediterranean*Meioherpia* Salv.-Pl. 1985*M. atlantica* Salv.-Pl. 1985 (type) Bermuda, off Beaufort, NC*M. stygalis* Salv.-Pl. 1985 Bermuda*Meiomenia* Morse 1979*M. (?) arenicola* Salv.-Pl. 1985 off coast of No. Carolina*M. swedmarki* Morse 1979 (type) San Juan Is., Puget Sound (Washington)

*Meromenia* Leloup 1949*M. hirondellei* Leloup 1949 (\*) Gulf of Gascogne*Metamenia* Thiele 1913*M. intermedia* Thiele 1913 (type) Davis Sea, Antarctic*M. triglandulata* Salv.-Pl. 1978 Ross Sea, Antarctic*Micromenia* Leloup 1948*Rupertomenia fodiens* Schwabl 1955 s.w. Sweden*M. simplex* Leloup 1948 (type) (\*) Arctic*Myzomenia* Simroth 1893 syn. *Nematomenia* Simroth 1893*Nematomenia* Simroth 1893*N. arctica* Thiele 1913 Spitzbergen*Dondersia banyulensis* Pruvot 1890 off Banyuls*N. banyulensis* var. *norvegica* Odhner 1921 Norway*Neomenia coralliophila* Kowalevsky 1881 Algeria*Dondersia flavens* Pruvot 1890 (type) off Banyuls (Mediterranean, Shetlands)*N. glacialis* Thiele 1913 Davis Sea, Antarctic*N. incirrata* Salv.-Pl. 1978 (\*) S. Orkney, Antarctic*Herpomenia platypoda* Heath 1911 Aleutian Islands*N. protecta* Thiele 1913 Davis Sea, Antarctic (juv.)*N. pytalosa* Salv.-Pl. 1978 So. Sandwich Is., Antarctic*N. squamosa* Thiele 1913 (\*) Davis Sea, Antarctic (juv.?)*N. tegulata* Salv.-Pl. 1978 So. Sandwich Is., Antarctic*Neomenia* Tullberg 1875*Solenopus affinis* Kor. & Dan. 1877 (\*) Messina*N. carinata* Tullberg 1875 (type) Sweden, Shetlands, Iceland*N. crenagulata* Salv.-Pl. 1978 (\*) nr. Kerguelen Isl.*Solenopus dalyelli* Kor. & Dan. 1877 Finmark, Scotland*N. grandis* Thiele 1894 (\*) Naples*N. herwigi* Kaiser 1976 s.w. Atlantic (off Falklands)*N. labrosa* Salv.-Pl. 1978 (\*) So. Shetland, Antarctic*N. laminata* Salv.-Pl. 1978 (\*) So. Orkney, Antarctic (juv.)*N. microsolen* Wirén 1892 (\*) West Indies*N. permagna* Salv.-Pl. 1978 (\*) [= ?*N. herwigi*] So. Pacific (55°S, 130°W) Antarctic*N. proprietecta* Salv.-Pl. 1978 (\*) juv. Ross Sea, Antarctic (juv.)*N. trapeziformis* Salv.-Pl. 1978 (\*) Antipodes Is., Antarctic*N. yamamotoi* Baba 1975 Hokkaido, Japan*Nierstraszia* Heath 1918*N. fragile* Heath 1918 off New Jersey*Notomenia* Thiele 1897*N. clavigera* Thiele 1897 (\*) Torres Straits

*Ocheyoherpia* Salv.-Pl. 1978

*O. linuifera* Salv.-Pl. 1978 So. Sandwich, So. Georgia, So. Shetland, Antarctic

*Pachymenia* Heath 1911

*P. abyssorum* Heath 1911 (\*) off So. California

*Paragymnomenia* Leloup 1947

*P. richardi* Leloup 1947 (\*) Mediterranean

*Paramenia* Pruvot 1890 syn. *Pruvotina* Cockerell 1903 (part.), *Eleutheromenia* 1967 (part.),  
*Macellomenia* Simroth 1893 (part).

*Pararrhopalia* Simroth 1893

*P. fasciata* Salv.-Pl. 1978 (\*) So. Shetlands, Antarctic

*Paramenia* (*Pararrhopalia*) *pruvoti* Simroth 1893 (type) Mediterranean

*Perimenia* Nierstrasz 1909 syn. *Pruvotina* Cockerell 1903*Pholidoherpia* Salv.-Pl. 1978

*Lepidomenia cataphracta* Thiele 1913 (type) Davis Sea, Antarctic

*P. lepidota* Salv.-Pl. 1978 (\*) Feuerland, Antarctic

*Phyllomenia* Thiele 1913

*P. austrina* Thiele 1913 (type) Antarctic

*P. cornuadenata* Salv.-Pl. 1978 Tierra del Fuego

*Plathymenia* Schwabl 1961

*P. branchiosa* Schwabl 1961 (\*) off So. California

*Proneomenia* Hubrecht 1880

*P. acuminata* Wirén 1892 n.w. Atlantic

*P. desiderata* Kow. & Marion 1887 Marseille

*P. epibionta* Salv.-Pl. 1978 nr. Falkland Is.; Antarctic

*P. filiformis* Hansen 1889 (\*) ?Norway

*P. gerlachei* Pelseneer 1901 (\*) Bellinghaus Sea, Antarctic

*P. hawaiiensis* Heath 1905 Hawaiian Is.

*P. insularis* Heath 1911 (\*) Hawaiian Is.

*P. langi* Simroth 1893 syn. *P. sluiteri* Hubrecht 1880

*P. nierstraszi* Stork 1940 syn. *Anamenia gorgonophila* Kow. 1881

*P. praedatoria* Salv.-Pl. 1978 Kerguelen Is., Tierra del Fuego

*P. sluiteri* Hubrecht 1880 (type) N.E. Atlantic

*P. stillerythrocytica* Salv.-Pl. 1978 Falkland Is.

*P. valdiviae* Thiele 1902 (\*) Indian Ocean, No. Zanzibar

*Proparamenia* Nierstrasz 1902

*P. bivalens* Nierstrasz 1902 Java Sea

*Pruvotia* Thiele 1894*Proneomenia sopita* Pruvot 1891 Banyuls*Pruvotina* Cockerell 1903*Paramenia cryophila* Pelseneer 1901 (\*fragment) Bellinghausen Sea, Antarctic*P. gauszi* Salv.-Pl. 1978 (\*) Davis Sea, Antarctic*Paramenia impexa* Pruvot 1890 (type) off Banyuls*P. longispinosa* Salv.-Pl. 1978 Antarctic*P. megathecata* Salv.-Pl. 1978 Tierra del Fuego*P. pallioglandulata* Salv.-Pl. 1978 So. Shetland Is., Antarctic*P. peniculata* Salv.-Pl. 1978 Tierra del Fuego, Ross Sea, Antarctic*P. praegnans* Salv.-Pl. 1978 So. Sandwich Is., So. Shetland Is., Antarctic*P. providens* Thiele 1913 (?) Davis Sea, Antarctic*P. uniperata* Salv.-Pl. 1978 Antarctic*Psammomenia* Swedmark (*nomen nudum*)*Rhabdoherpia* Salv.-Pl. 1978*R. ventromusculata* Salv.-Pl. 1978 Ross Sea, Antarctic*Rhipidoherpia* Salv.-Pl. 1978*R. copulobursata* Salv.-Pl. 1978 Kerguelen Is.*Rhopalomenia* Simroth 1893*Proneomenia aglaopheniae* Kow. & Mar. 1887 (type) Mediterranean, so. England*Entonomenia atlantica* Leloup 1948 (\*) Tenerife*R. carinata* Salv.-Pl. 1978 So. Georgia, So. Shetland, Antarctic*R. cristata* Salv.-Pl. 1978 Antarctic*R. eisigi* Thiele 1894 syn. *R. aglaopheniae* Kow. & Mar. 1887*R. rhynchopharyngeata* Salv.-Pl. 1978 Antarctic*R. sertulariicola* Salv.-Pl. 1978 So. Sandwich, Antarctic*R. tricarinata* Salv.-Pl. 1978 Antarctic*Rupertomenia* Schwabl 1955 syn. *Micromenia* Leloup 1948*Sandalomenia* Thiele 1913*S. carinata* Thiele 1913 (\*) Davis Sea, Antarctic (juv.)*S. papilligera* Thiele 1913 (type) Davis Sea, Antarctic*Sialoherpia* Salv.-Pl. 1978*S. aculeitecta* Salv.-Pl. 1978 (\*) Drake Str.*Simrothiella* Pilsbry 1898*Solenopus margaritaceus* Kor. & Dan. 1877 (type) (Odhner, 1921) Norway*S. rhynchota* Salv.-Pl. 1978 (\*) So. Pacific (56°S, 156°W)*S. schizoradulata* Salv.-Pl. 1978 Drake Str., off Peru

*Solenopus* M. Sars 1969 syn. *Simrothiella* Pilsbry 1898 (part.), *Dorymenia* Heath 1911 (part.), *Neomenia* Tullberg 1875 (part.)

*Spengelomenia* Heath 1912

- S. bathybia* Heath 1912 (\*) off Florida
- S. intermedia* Salv.-Pl. 1978 (\*) Drake Str., Antarctic
- S. polypapillata* Salv.-Pl. 1978 (\*) Scotia Sea, Antarctic
- S. procera* Salv.-Pl. 1978 Drake Str., Antarctic

*Sputoherpia* Salv.-Pl. 1978

- S. exigua* Salv.-Pl. 1978 So. Pacific (55°S, 130°W) (juv.)
- S. fissitubata* Salv.-Pl. 1978 (\*) E. of Kerguelen
- S. laxopharyngeata* Salv.-Pl. 1978 S.E. Atlantic (35°S, 17°E)
- S. megaradulata* Salv.-Pl. 1978 (\*) Scotia Sea, Antarctic

*Strophomenia* Pruvot 1899

- Rhopalomenia debilis* Nierstrasz 1902 (\*immature) Buton Str.
- Rhopalomenia indica* Nierstrasz 1902 E. Indian Arch.
- Strophomenia lacazei* Pruvot 1899 (type) Algeria
- S. ophidiana* Heath 1911 (\*) So. of Honshu, Japan
- S. regularis* Heath 1911 (\*fragment) So. of Honshu
- S. scandens* Heath 1911 Hawaiian Is.

*Stylomenia* Pruvot 1899

- S. salvatori* Pruvot 1899 Mediterranean

*Syngenoherpia* Salv.-Pl. 1978

- S. intergenerica* Salv.-Pl. 1978 (type) So. Pacific (55°S, 130°W)
- S. sanguicuneosa* Salv.-Pl. 1978 Balleny Is., Antarctic
- Proneomenia thulensis* Thiele 1900 (\*) (juv.) Spitzbergen

*Tegulaherpia* Salv.-Pl. 1983

- T. myodoryata* Salv.-Pl. 1988 western Mediterranean
- T. stimulosa* Salv.-Pl. 1983 (type) eastern Mediterranean
- T. tasmanica* Salv.-Pl. 1988 Bass Strait, Australia

*Uncimenia* Nierstrasz 1903

- U. neapolitana* Nierstrasz 1903 (\*) Naples

*Utralvoherpia* Salv.-Pl. 1978

- U. abyssalis* Salv.-Pl. 1978 (\*) So. Orkney, Antarctic

*Vermiculus crassus* Dalyell syn. *Neomenia* sp. (?*N. dalyelli* K & D 1877)

*Wirenia* Odhner 1921

- W. argentea* Odhner 1921 (\*) Norway

\*single specimen

## Appendix B. Named Genera and Species of Chaetodermomorpha

*Caudofoveatus* Ivanov 1981

- C. callosus* Ivanov 1984 Peter the Great Bay (Sea of Japan) 35-93 m  
*C. tetrads* Ivanov 1981 (type) White Sea 70 m

*Chaetoderma* Lovén 1844

- C. abidjanense* Scheltema 1976 off Ivory Coast 80 m  
*C. akkesiense* Okuda 1943 Akkeshi Bay, Japan 54 m  
*C. araucanae* Osorio & Tarifeño 1976 Valparaiso Bay, Chile 119-145 m  
*C. argenteum* Heath 1911 (\*) So. Alaska, Oregon, California 70-640 m  
*C. attenuatum* Heath 1911 syn. *C. argenteum* Heath 1911  
*C. bacillum* Heath 1918 S.E. Cape Cod, Massachusetts 1,631 m  
*C. californicum* Heath 1911 (\*) nr. San Diego, California 1,112-1,201 m  
*C. canadense* Nierstrasz 1902 syn. *C. nitidulum* Lovén  
*Crystallophrisson chistikovi* Ivanov 1986 Chukchi Sea 280 m  
*C. eruditum* Heath 1911 So. Alaska 508-563 m  
*Crystallophrisson glacialis* Ivanov 1986 Chukchi Sea 470 m  
*Crystallophrisson hancocki* Schwabl 1963 So. California 43-803 m  
*C. hawaiiense* Heath 1911 off Kauai Is., Hawaii 509-950 m  
*Crystallophrisson incrassatum* Schwabl 1963 So. California 495-549 m  
*Crystallophrisson indicum* Stork 1941 (\*) W. Pacific (9°S, 120°E) 959 m  
*Crystallophrisson inflatum* Schwabl 1963 syn. *C. hancocki* (Schwabl 1963)  
*C. intermedium* Knipowitsch 1896 White Sea 20-350  
*C. japonicum* Heath 1911 (\*) off Honshu, Japan 373-450 m  
*Crystallophrisson kasanovi* Ivanov 1984 Sea of Japan 33-69 m  
*C. lucidum* Heath 1918 N.W. Atlantic 770-862 m  
*Crystallophrisson luitfriedi* Ivanov 1987 No. Sea 40-60 m white  
*C. majusculum* Scheltema 1976 off Ivory Coast 100-300 m  
*Crystallophrisson marinae* Ivanov 1987 No. Sea 150-264 m white  
*Crystallophrisson marinelli* Schwabl 1963 So. California 29-772 m  
*Crystallophrisson marioni* Stork 1941 (\*) W. Pacific (6°S, 120°E) 462 m  
*C. militare* Selenka 1885 (\*) Philippines 655 m  
*C. montereyense* Heath 1911 syn. *C. argenteum* Heath 1911  
*C. nanulum* Heath 1911 off So. California 160-600 m  
*Crystallophrisson nitens* Möbius 1874 syn. *C. nitidulum* Lovén 1844  
*C. nitidulum* Lovén 1844 (type) E&W north Atlantic about 40-450 m  
*Crystallophrisson nitidulum* var. *pacifica* Schwabl 1963 So. California 22-233 m  
*Crystallophrisson orientale* Stork 1941 (\*) W. Pacific 10°S, 123°E 918 m  
*C. productum* Wiren 1892 Arctic 95-405 m  
*Crystallophrisson recisum* Schwabl 1963 (\*) San Pedro, California 477 m  
*Crystallophrisson rectum* Schwabl 1963 ?syn. *C. hancocki* (Schwabl 1963)  
*Crystallophrisson riedli* Schwabl 1963 syn. *C. nanulum* Heath 1911

- C. robustum* Heath 1911 so. of Alaska Peninsula 869 m  
*Crystallophrisson rubrum* Schwabl 1963 (\*) ?syn. *C. nanulum* Heath 1911  
*C. scabrum* Heath 1911 (\*) Monterey Bay, Calif. 180-1,568 m  
*Crystallophrisson scheltemae* Ivanov 1984 Sea of Japan 65-140 m  
*Crystallophrisson sibogae* Stork 1941 (\*) W. Pacific 5°S, 122°E 1,886 m  
*C. simplex* Salv.-Pl. 1971 (\*) off SW Greenland 2,258 m  
*C. squamosum* Heath 1918 S.E. of Cape Cod, Massachusetts 2,221 m  
*C.? strigisquamatum* Salv.-Pl. 1977 (\*) W. Mediterranean, 1491 m  
*C. usitatum* Scheltema 1989 off SE Australia 1200-1850 m  
*C. vadorum* Heath 1918 syn. *C. nitidulum* Lovén

#### *Chevroderma* Scheltema 1985

- C. gausson* Scheltema 1985 northern West European Basin greater than 4,000 m  
*C. scalpellum* Scheltema 1985 eastern Atlantic 10°N-10°S 1,427-2,644 m  
*C. turnerae* Scheltema 1985 (type) Atlantic 2,100-5,208 m  
*C. whitlatchi* Scheltema 1985 eastern no. Pacific 2,800-7,298 m

#### *Falcidens* Salv.-Pl. 1968

- F. aequabilis* Salv.-Pl. 1972 Mediterranean 132-3,542 m  
*Chaetoderma afanasjevi* Ivanov 1986 Chukchi Sea 240 m  
*Chaetoderma caudatum* Heath 1918 N.W. Atlantic 203-1,437 m  
*F. chistos* Scheltema 1989 Bass Str. 22-120 m  
*F. crossotus* Salv.-Pl. 1968 (type) Norwegian fjords and basin; West European Basin 29-470 m  
*Chaetoderma gutturosum* Kowalevsky 1901 Mediterranean 40-866 m  
*Crystallophrisson hartmani* Schwabl 1961 So. California 330-1,100 m  
*Chaetoderma hoffmanni* Stork 1939 (\*) locality unknown  
*F. ingolfensis* Salv.-Pl. 1971 No. Atlantic (sw of Greenland) 2,258 m  
*F. liosquameus* Salv.-Pl. 1969 Red Sea ?m  
*F. lipuros* Scheltema 1989 Bass Str. 120-130 m  
*Chaetoderma loveni* Nierstrasz 1902 Java Sea 1,310 m  
*F. macrafrondis* Scheltema 1989 off SE Australia, 1,200 m  
*Chaetoderma moskalevi* Ivanov 1986 Chukchi Sea 240 m  
*Chaetoderma normanni* Nierstrasz 1902 (\*) locality unknown  
*Crystallophrisson odhneri* Stork 1941 (\*) W. Pacific, 9°S, 120°E 959 m  
*Chaetoderma pellucida* Ivanov 1987 White Sea 65-90 m  
*F. profundus* Salv.-Pl. 1971 No. Atlantic (SW of Greenland) 2,258 m  
*F. sagittiferus* Salv.-Pl. 1968 Norwegian fjords and Basin 30-680 m  
*Chaetoderma salviniplaweni* Ivanov 1984 Sea of Japan 66-70 m  
*Crystallophrisson sterreri* Salv.-Pl. 1967 W. Sweden, Norwegian fjords 30 m [?]  
*F. thorensi* Salv.-Pl. 1971 No. Atlantic 1,096-2,150m  
*Chaetoderma wireni* Nierstrasz 1902 (\*) Banda Sea 1,570 m

#### *Limifossor* Heath 1904

- L. fratula* Heath 1911 S. California 144-810 m  
*L. talpoideus* Heath 1904 (type) Alaska 540 m  
*Limifossor* sp. [Scheltema 1981] off Florida



*Metachaetoderma* Thiele 1913*Chaetoderma challenger* Nierstrasz 1902 [?Western Atlantic 702-2,250 m]*Prochaetoderma* Thiele 1902*Chaetoderma radulifera* Kowalevsky 1901 (type) Mediterranean 54-2,415 m*P. yongei* Scheltema 1985 NW, NE and SE Atlantic 450-2,200 m*Psilodens* Salv.-Pl. 1977*Limifossor elongatus* Salv.-Pl. 1972 (type) off Panama, Costa Rica, Ecuador 1,609-3,757 m*P. tenuis* Salv.-Pl. 1977 off Straits of Gibraltar (Atlantic) 2,500 m*Rhabdoderma* Scheltema 1989*R. australe* Scheltema 1989 (type) off SE Australia 1,120-2,510 m*Scutopus* Salv.-Pl. 1968*S. chilensis* Salv.-Pl. 1972 off Chile to Straits of Magellan 263-642 m*S. megaradulatus* Salv.-Pl. 1972 Caribbean, off Cape Hatteras, No. Carolina 650-974 m*S. robustus* Salv.-Pl. 1970 Norwegian fjords and Basin, Mediterranean Sea 200-3,542 m*S. ventrolineatus* Salv.-Pl. 1968 (type) E. Atlantic, Norway to Durban, Africa 40-1,248 m*Spathoderma* Scheltema 1985*Prochaetoderma californicum* Schwabl 1963 S. Calif. 527-817 m*S. clenchi* Scheltema 1985 (type) NW, NE & SE Atlantic 1,470-3,356 m

**Appendix C. Aplacophorans Examined by A. Scheltema from Recent Atlantic Expeditions  
and Surveys Listed North to South**

Survey/ Expedition	Date	Location	Depth range to nearest 100 m	No. Specimens	Authors if published
<b><u>WESTERN ATLANTIC</u></b>					
NORATLANTE <sup>1</sup>	?	Labrador B.	3500-4100	17	
		Newfoundland B.	5200	2	
CHAIN 106 <sup>2</sup>		Newfoundland B.	3800-4800	242	Scheltema 1985a (part)
OCEANUS 88, 91, 95 <sup>2</sup>	1985?	Georges Bank	100-2000	106	
VERRILL 67-53 <sup>2</sup>	Aug 1967	Gulf of Maine	160	24	
MBL <sup>3</sup>	Feb 1966- Oct 1969	Cape Cod Bay	<100	30	Scheltema 1972, 1973
WHOI <sup>2,4</sup>	1960-77	Gay Head-Bermuda	200-5000	~4500 <sup>5</sup>	Scheltema 1985a (part)
ALVIN <sup>2,6</sup>	1972-78, Sep 1989	off New York	1800, 2500, 3600	286	Scheltema 1985a (part)
MMS <sup>7</sup>	1984-85	off Delaware/NJ	1500-2500	Numerous	Maciolek et al. 1986 (Prochaeto- dermatidae only)
EASTWARD <sup>8</sup>	1965	off Cape Hatteras	400-600	67	
Florida Coastal Studies <sup>9</sup>	1978-81	off Ft. Pierce, FL	100-200	290	
ALVIN <sup>2,10</sup>	1974-?	Blake Plateau	2000	27	
KNORR 25 <sup>2</sup>	Feb-Mar 1972	Guiana B.	500-5000	394	
DEMERABY <sup>1</sup>	Sep-Oct 1980	off Guiana	4400, 4800	20	
ATLANTIS II-31 <sup>2</sup>	Feb 1967	Brazil B.	600-1500	396	
GEOCOSTA RIO II <sup>11</sup>	1986	off Rio de Janeiro	<100	26	Scheltema 1990
ATLANTIS II-60 <sup>2</sup>	Mar 1971	Argentine B.	250-5200	1252	Scheltema 1985a (part)

Appendix C. (continued)  
 e 2

Survey/ Vessel	Date	Location	Depth range to nearest 100 m	No. Specimens	Authors if published
<b><u>MID-ATLANTIC RIDGE</u></b>					
ATLANTIC <sup>1</sup>	?	off Azores	3600	16	
OVEMA <sup>1</sup>	Nov 1977	bet. Dakar-Caracas	800-1900	48	
<b><u>EASTERN ATLANTIC &amp; MEDITERRANEAN</u></b>					
CAL <sup>1</sup>	July-Aug 1976	off Scotland	600-2500	1245	Scheltema 1985a, Scheltema et al. 1989 (part); See Appendix E herein
		off Ireland	2900	656	
		W. of Brest	4200-4800	677	
RAIN 106 <sup>2</sup>	Aug 1972	off Ireland	500-4600	586	Scheltema 1985a (part)
ATLANTIC <sup>1</sup>	?	off Ireland	2500	2	
		Bay Biscay	2000-4700	60	Scheltema 1985a,b (part)
		W. of Gibraltar	2600	7	
RSIA <sup>12</sup>	Jul 1967	Bay Biscay	100-2400	496	Scheltema 1985a,b (part)
ALASSA 70, 1, 72, 73 <sup>1</sup>	1970-73	Bay Biscay	200-2100	427	Scheltema 1985a,b (part)
LYGAS, IOGAS I-XI <sup>1</sup>	Aug 1972- Oct 1981	Bay Biscay	100, 1000-4700	1828	Scheltema 1985a,b (part)
YPLAINE <sup>1</sup>	May-Jun 1981, Jul 1983	Iberian B.	4200-5300	214	
LGIM <sup>1</sup>	May-Jun 1984	W. Medit., Gibraltar, Iberian B.	140-2100	787	
LYMEDE <sup>1</sup>	?	W. Medit.	2100-2900	83	
PLANTIS II-59 <sup>2</sup>	Sep 1970	E. Medit.	500-1500	82	
SCOVERY <sup>12</sup>	Mar 1968	off Canaries	1600-3000	40	Scheltema 1985a (part)

Appendix C. (continued)  
Page 3

Survey/ Expedition	Date	Location	Depth range to nearest 100 m	No. Specimens	Authors if published
<b><u>EASTERN ATLANTIC &amp; MEDITERRANEAN (continued)</u></b>					
ATLANTIS II-31 <sup>2</sup>	Feb 1967	off Dakar	1600-3900	337	Scheltema 1985a (part)
WALDA <sup>1</sup>	Jun-Jul 1971	off Africa, Guinea-Namibia	1300-4300	303	Scheltema 1985a (part)
ATLANTIS II-42 <sup>2</sup>	May 1968	off Luanda  off Walvis Bay	200-4600	1734	Scheltema 1985a (part), Scheltema et al. 1989 (part)
WALVIS <sup>1</sup>	Dec 1978- Jan 1979	Walvis Ridge	3600-5300	61	

Footnotes

1. Centre National de Tri d'Océanographie Biologique (CENTOB), Brest, France.
2. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.
3. Marine Biological Laboratory, Woods Hole, Massachusetts, Systematics-Ecology Program.
4. R.V. ATLANTIS Cruise 263, 273, 277, 283, 284, 298; ATLANTIS II 12, 17, 23, 24, 30, 40; CHAIN 50, 58, 88; KNORR 35; OCEANUS 10.
5. Three species of Prochaetodermatidae (Scheltema 1985a) account for 75 percent of the total specimens.
6. Dives 328, 407, 408, 459, 460, 773, 774, 776, 794, 834, 2161-2167.
7. Battelle Laboratory for Minerals Management Service, U.S. Department of Interior.
8. Duke University Marine Laboratory, Beaufort, North Carolina.
9. Harbor Branch Laboratory, Ft. Pierce, Florida.
10. Dives 492, 563, 752-754, 849, 1072.
11. Instituto de Biologia, Universidade Federal do Rio de Janeiro.
12. National Institute of Oceanography, U.K.

# Appendix D. Major Expeditions and Surveys which Have Collected Aplacophora in the Pacific (Scheltema, 1990).

52

BULLETIN OF MARINE SCIENCE, VOL. 47, NO. 1, 1990

Survey/expedition†	Date	Location/depth m	Specimens (No.)	Species† (No.)	Authors, if published
SIBOGA Exp.	1899-1900	East Indies 18-3,088	66	~13	Nierstrasz, 1902; Stork, 1941
ALBATROSS Exp.	1891, 1902	off Hawaii 9-275	18	7	Heath, 1911
ALBATROSS Exp.	1892, 1906	No. Pacific, Kuriles, Alaska 122-868	17	3	Heath, 1911
ALBATROSS Exp.	1897, 1904	off so. California 38-3,953	199	10	Heath, 1911
ALBATROSS Exp.	1903	So. Alaska (panhandle) 90-527	22 + "several"	3	Heath, 1911
ALBATROSS Exp.	1906	off Japan 185-413	18	7	Heath, 1911
Allan Hancock Pacific Exp.	1952-1957	off so. California 33-1,102	283	14	Schwabl, 1963
VEMA Exp.; U.S. Antarctic Res. Pgm.	1958-1961, 1964	off Central, So. America 626-5,834	11	3	Salvini-Plawen, 1972, 1978
U.S. Antarctic Res. Pgm.	1964-1966	So. Pacific 146-3,694	39	9	Salvini-Plawen, 1978
Univ. Oregon‡	1962-1967	off Oregon 100-2,900	276	~12	unpubl.
SSR Academy Nauk	1970	Peter the Great Bay 120	42	4	Ivanov, 1984
SEVENTOW	1970	Aleutian Trench 7,298	31	1	Scheltema, 1985
DOMES Project	1975-1976	mid-Pacific 4,985-5,117	3	1	Scheltema, 1985
So. California‡ Bight Pgm.	1976	off Los Angeles, California	143+	10+	unpubl.
SEATECH‡	1981	off British Columbia 107-175	205	3	unpubl.
DSRV ALVIN	1981-1982	Panama Basin 4,000	59	~5	Scheltema, 1985 (part)
Bass Str. Sur- vey,‡ Mus. Victoria	1980-1983	Bass Strait <200	382	~25	Scheltema, 1989 (part)
CSIRO-FRS- 86‡	1986	Slope off SE Australia 363-1,850	937	>40	Scheltema, 1989 (part)

\* Single species or specimens not included in the table but indicated on Figure 1 are described in Selenka (1885: Philippines), Thiele (1897, 1902: Torres Strait, s.w. Australia, East Indies), Ponder (1970: off New Zealand), Baba (1940, 1975: Japan), Okuda (1943: Japan), Osorio and Tariffa (1974: Chile), Morse (1979: Puget Sound, intertidal). Species to be described have been taken from sea mounts in the eastern Pacific (13 specimens, 7 spp.), from Panama Bay (25 specimens, 1 spp.), from New Caledonia (4 specimens, 2 spp.), and from the Great Barrier Reef (3 specimens, 2 spp.). Most of the more than 700 specimens and 14 species from hydrothermal vents are listed in Table 3.

† CSIRO = Australian Commonwealth Scientific and Industrial Research Organization; SEVENTOW = R.V. Albatross Cruise 70, Scripps Institution of Oceanography; DOMES was a project under the National Oceanographic and Atmospheric Administration, U.S. Department of Commerce; SEATECH was a project under the Canadian Department of Fisheries and Oceans; So. California Bight Pgm. was under Minerals Management Service, U.S. Department of Interior.

‡ Species known or suspected to be synonyms in Siboga, Albatross, and Allan Hancock samples are not included. The same species may occur in more than one collection.

§ Collections with unpublished species examined for the present paper.

**Appendix E. Preliminary Aplacophoran Identifications from One Expedition in the West European Basin: INCAL, Centre Océanologique de Bretagne, Brest. Many Species Formed the Basis for Scheltema et al. 1989. The Prochaetodermatidae Have Been Published (Scheltema 1985) and Are Not Included.**

Locality	Stn	Depth m	No. Specimens	Identification
I	DS-01	2091	31	Dondersiidae
			16	<i>Plawenia</i> n.g.
			35	Pholidoskepia:
				6 elongate smooth
				10 oily sheen
				4 elongate, rough
				15 cf. <i>Gymnomenia</i>
			17	Pararrhopalidae, short, v. spiny; > 1 species?
			8	<i>Acanthomenia</i>
			4	Smooth, skeletal spicules
			15	Neomeniomorpha
			3	<i>Macellomenia</i> A
			3	<i>Chaetoderma</i> - 3 spp.
I	DS-02	2081	26	<i>Plawenia</i> n.g.
			24	<i>Acanthomenia</i>
			10	<i>Uncimenia</i>
			10	Pararrhopalidae, spiny
			3	Pholidoskepia elongate
			4	<i>Kruppomenia</i>
			5	Proneomeniidae
			4	Neomeniomorpha
			5	<i>Chaetoderma</i> - 3 spp.
			3	<i>Uncimenia</i>
I	CP-01	2040	2	Smooth, elongate, skeletal spicules
			1	Pholidoskepia
			2	Pararrhopalidae
			4	<i>Plawenia</i> n.g.
			4	<i>Acanthomenia</i>
			9	<i>Chaetoderma</i> - 4 spp.
			1	Chaetodermomorpha
I	CP-02	2091	1	<i>Plawenia</i> n.g.
			2	<i>Acanthomenia</i>
			2	<i>Uncimenia</i>
			14	<i>Chaetoderma</i> - 3 spp.
			7	<i>Kruppomenia</i>
II	DS-03	609	12	Neomenioid fragments
			Many	<i>Archaeomenia</i>
			17	Pholidoskepia
			1	Proneomeniidae

Appendix E. (continued)  
Page 2

Locality	Stn	Depth m	No. Specimens	Identification
II	DS-04	619	1	<i>Archaeomenia</i>
			4	Neomenioids undet.
			2	Pholidoskepia
			2	Smooth, skeletal spicules
			2	Fragments
III	DS-05	2503	20	Pararrhopalidae spiny
			14	<i>Uncimenia</i>
			1	<i>Plawenia</i> n.g.
			2	Spheres, skeletal spicules
			2	Undet. juveniles
			24	<i>Kruppomenia</i> B
			9	<i>Acanthomenia</i>
			2	Neomenioida "new"
			6	Neomeniomorpha - 4 spp.
			3	Pholidoskepia
III	DS-06	2494	11	Spheres, skeletal spicules
			18	<i>Kruppomenia</i> B
			6	<i>Uncimenia</i> - 2 spp.
			4	<i>Acanthomenia</i>
			4	Neomeniomorpha - 3 spp.
			10	Pararrhopalidae
			6	Pholidoskepia
			3	<i>Acanthomenia</i>
III	CP-03	2466	3	<i>Chaetoderma</i>
			3	<i>Chaetoderma</i>
III	CP-04	2483	1	Proneomeniidae
			1	<i>Acanthomenia</i>
			1	Pararrhopalidae
			5	<i>Chaetoderma</i> - 2 spp.
IV	DS-07	2884	71	Pararrhopalidae - 2 spp.
			2	Proneomeniidae
			1	<i>Uncimenia</i>
			2	Pholidoskepia
			14	<i>Acanthomenia</i>
IV	DS-08	2891	21	Pararrhopalidae
			3	Pholidoskepia
			4	<i>Acanthomenia</i>
			3	Spheres, skeletal spicules
			1	Neomeniomorpha
			4	<i>Uncimenia</i>

Appendix E. (continued)  
Page 3

Locality	Stn	Depth m	No. Specimens	Identification
IV	DS-09	2897	190	Pararrhopalidae
			17	<i>Acanthomenia</i>
			10	cf. <i>Plawenia</i> n.g.
			1	Large Pararrhopalidae
			24	<i>Uncimenia</i>
			7	<i>Kruppomenia</i>
			9	<i>Pholidoskepia</i> - 2 spp.
			1	<i>Chaetoderma</i>
			4	<i>Uncimenia</i>
IV	CP-05	2884	3	<i>Acanthomenia</i>
			2	<i>Pholidoskepia</i>
			9	Pararrhopalidae
			1	<i>Chaetoderma</i>
			6	<i>Uncimenia</i>
IV	CP-06	2888	9	<i>Acanthomenia</i>
			2	<i>Pholidoskepia</i>
			16	Pararrhopalidae
			2	Neomeniomorpha
			7	<i>Chaetoderma</i> - 2 spp.
			51	Pararrhopalidae
			9	<i>Pholidoskepia</i>
IV	CP-07	2895	1	Sphere, skeletal spicules
			4	<i>Acanthomenia</i>
			9	<i>Uncimenia</i>
			1	Neomeniomorpha, skeletal spicules
			10	<i>Chaetoderma</i> - 2 spp.
			1	<i>Chaetoderma</i>
			3	Fragments
V	DS-10	2719	2	<i>Kruppomenia</i> A
V	CP-08	2644	9	<i>Uncimenia</i>
			3	Pararrhopalidae
			3	Neomeniomorpha - 3 spp.
			8	<i>Acanthomenia</i> - 2 spp.
			12	<i>Pholidoskepia</i>
			2	<i>Chaetoderma</i>
V	CP-09	2659	5	<i>Uncimenia</i>
			3	Neomeniomorpha - 3 spp.
			2	Pararrhopalidae
			2	<i>Pholidoskepia</i>
			1	<i>Chaetoderma</i>



Appendix E. (continued)  
Page 4

Locality	Stn	Depth m	No. Specimens	Identification
V	ØS-01	2634	4	<i>Uncimenia</i> - 2 spp.
			2	Neomenioida "new" - 2 spp.
			3	<i>Kruppomenia</i>
			1	<i>Acanthomenia</i>
			6	Neomeniomorpha, skeletal spicules
			1	<i>Macellomenia</i>
			2	Neomeniomorpha, squat, spiny
			4	Pararrhopalidae
			6	Pholidoskepia
			1	<i>Chaetoderma</i>
V	WS-01	2550	10	Neomeniomorpha, skeletal spicules - 2 spp.
			12	<i>Uncimenia</i>
			1	Spheres, skeletal spicules
			16	Pararrhopalidae
			2	<i>Acanthomenia</i>
			1	Neomenioida "new"
			3	Pholidoskepia
			1	Proneomeniidae
			3	<i>Chaetoderma</i> - 2 spp.
V	WS-02	2498	16	Pararrhopalidae - 2 spp.
			36	Pholidoskepia
			31	<i>Macellomenia</i>
			5	Neomeniomorpha - 2-4 spp.
			2	Neomenioida "new"
			3	<i>Chaetoderma</i> - 2 spp.
VI	DS-11	4823	2	Fragments
VI	CP-10	4823	2	Neomeniomorpha
VI	CP-11	4823	1	Neomeniomorpha
VI	ØS-02	4829	1	<i>Acanthomenia</i>
			1	<i>Uncimenia</i>
			1	Pararrhopalidae
			3	Neomeniomorpha - 3 spp.
VI	WS-03	4829	1	<i>Acanthomenia</i>
			1	<i>Uncimenia</i>
			1	Proneomeniidae
			4	Small specimens

Appendix E. (continued)  
Page 5

Locality	Stn	Depth m	No. Specimens	Identification
VI	WS-04	4829	1	Pararrhopalidae
			1	Proneomeniidae
			1	Neomeniomorpha
VII	DS-13	4822	4	Neomeniomorpha, spicules lacking
VII	CP-13	4800	1	Neomeniomorpha
VII	ØS-03	4789	1	Proneomeniidae
			2	<i>Acanthomenia</i>
			1	Pararrhopalidae
			1	Neomeniomorpha
VII	ØS-04	4796	1	Pararrhopalidae
			1	<i>Acanthomenia</i>
			2	Neomeniomorpha - 2 spp.
VII	WS-05	4804	7	Pholidoskepia - 2 spp.
			12	Neomeniomorpha - 5 spp.
			4	Pararrhopalidae
			?	<i>Uncimenia</i> - 2 spp.
			4	Neomenioida "new"
			2	<i>Macellomenia</i>
VIII	DS-14	4254	1	<i>Krappomenia</i> A
			1	Neomenioida "new"
			7	Neomeniomorpha, poor condition
VIII	DS-15	4211	1	<i>Krappomenia</i> A
			1	? <i>Acanthomenia</i>
VIII	DS-16	4268	4	<i>Krappomenia</i> A
			11	Pararrhopalidae - 4 spp.
			29	Neomeniomorpha - several spp.
			4	Pholidoskepia
			8	Neomenioida "new"
			10	<i>Acanthomenia</i>
VIII	ØS-05	4296	1	<i>Chaetoderma</i>
			1	Neomeniomorpha
VIII	ØS-06	4316	7	<i>Krappomenia</i>
			15	Neomeniomorpha - 5 or more spp.
			4	Neomenioida "new"
			3	<i>Uncimenia</i> & Pararrhopalidae
			1	<i>Acanthomenia</i>

Appendix E. (continued)  
Page 6

Locality	Stn	Depth m	No. Specimens	Identification
VIII	ØS-07	4249	15	Spiny Neomeniomorpha
			6	<i>Krappomenia</i> A
			3	Pholidoskepia
			?	Pararrhopalidae
			?	<i>Uncimenia</i>
			4	<i>Acanthomenia</i>
			9	Neomenioida "new"
VIII	ØS-08	4327	12	Neomeniomorpha - several spp.
			55	Neomeniomorpha - 2 spp.
			4	<i>Krappomenia</i> A
			9	Neomenioida "new"
			3	<i>Acanthomenia</i>
			4	Pholidoskepia
VIII	WS-07	4281	16	<i>Uncimenia</i> , Pararrhopalidae
			3	<i>Acanthomenia</i>
			3	<i>Uncimenia</i>
VIII	WS-08	4287	2	Neomeniomorpha - 2 spp.
			3	<i>Uncimenia</i> , Pararrhopalidae - 3 spp.
			2	Neomenioida "new"
			1	<i>Acanthomenia</i>
			1	Proneomeniidae
VIII	WS-09	4277	1	Pholidoskepia
			2	Neomenioida "new"
			1	<i>Plawenia</i> n.g.
			4	Pholidoskepia
			1	Pararrhopalidae
			2	<i>Acanthomenia</i>
VIII	WS-10	4354	7	Neomeniomorpha - 2 spp.
			1	Neomeniomorpha
			1	<i>Acanthomenia</i>

## Appendix F. Characters Used for Descriptions of Aplacophora

Character	State
<b>I Neomeniomorpha</b>	
<b>A. External and hard parts</b>	
Body	Shape, dimensions, carinate or not
Mouth	Shape, proboscis present/absent
Mantle cavity	Shape of opening, spicule arrangement
Foot groove	Spicule arrangement
Pedal pit	Size
Dorsoanterior sense organ(s)	Present/absent, visibility
Dorsoterminal sense organ(s)	Present/absent, visibility
Spicule arrangement	Upright, flatlying, skeletal
Spicules	Shape, solid/hollow
Radula	Type, shape, dimensions, no. rows, no. teeth,
Copulatory spicules	Present/absent, shape, number, dimensions
Accessory copulatory spicules	Present/absent, shape, number, dimensions
<b>B. Internal soft anatomy</b>	
Cuticle	Thickness
Epidermis	Thickness, cell types
Epidermal papillae	Stalked/unstalked, shape
Dorsoanterior sense organ	Present/absent, shape
Body-wall musculature	No. of layers, thickness
Vestibular papillae	No., shape
Mouth	Separate/joined with vestibule
Foot	No. folds
Pedal pit	Size, shape, cell types, ciliation
Oral tube walls	Folded/smooth
Sensory macrocilia	Present/absent in vestibule, oral tube
Dorsal salivary gland(s)	Diffuse follicles/gland with duct
Pharyngeal wall	Folded/smooth
Ventral salivary glands (paired)	Shape, size, duct single or paired/absent
Dorsal cecum	Size, paired or single/absent
Esophagus	Present/absent
Anteroventral radular pocket	Present, paired or single/absent
Midgut contents	Type of food, shape of nematocysts if present
Midgut sacculations	Present/absent
Gonad	Deviation from usual
Pericardium	Size, relationship to ducts of reproductive system
Heart	Size, attached/free
Seminal vesicles	Present/absent, location

**Appendix F. (continued)**  
**Page 2**

Character	State
Seminal receptacles	Present/absent, shape, location
Upper and lower gametoducts	Course, cell types, ciliation, fusion
Spermatophores	Present/absent
Gametopore(s)	Single/paired
Copulatory spicule pockets	Present/absent, shape, extent, glands
Mantle cavity	Pockets, extent/absent
	Respiratory folds, papillae
	present/absent, shape, no.
	Brood chamber present/absent
	Glands present/absent
Dorsoterminal sense organ(s)	Present/absent, shape
Nervous system	Deviation from usual
<b>II Chaetodermomorpha</b>	
<b>External hardparts</b>	
Body	Shape, dimensions, ratios of body regions
Oral shield	Shape, size relative to body diameter, location of mouth
Anterior constriction	Present/absent, weak/strong
Mantle cavity	Shape, spicule arrangement
Dorsoterminal sense organ	Size, visibility
Spicule arrangement	Erect, flatlying, direction
Spicules	Shape, dimensions by body region
Radula	Shape, dimensions, no. rows, no. denticles
Jaws (Prochaetodermatidae)	Shape, dimensions



## **Appendix G. Curriculum Vitae, Amélie H. Scheltema**

### **Education**

A.B., Bryn Mawr College, Bryn Mawr, PA, 1950; major, geology  
 University of Colorado, Boulder, Co, 1949; summer field course in geology  
 Radcliffe College, Cambridge, MA, 1954; graduate work in geology  
 Boston University Marine Program, Woods Hole, MA, fall 1969; graduate course in invertebrate zoology

### **Fellowships and Awards**

Scholar, Radcliffe Institute, Cambridge, MA, 1965-1967  
 Grant, Conchologists of America, 1989

### **Professional Societies**

American Association for Zoological Nomenclature  
 American Malacological Union  
 Biological Society of Washington  
 Malacological Society of London  
 Sigma Xi  
 Unitas Malacologica  
 Western Society of Naturalists

### **Employment**

Junior Geologist - U.S. Geological Survey, Washington, DC, 1951-1954  
 Editorial Staff - Ginn and Company, Boston, MA, 1955-1956  
 Editorial Staff - University of North Carolina Press, Chapel Hill, NC, 1957-1959  
 Free lance - various short-term laboratory employment and scientific editorial work, 1956-1964  
 Editor (part-time) Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, 1961-1965  
 Instructor - summer workshop for science teachers, Falmouth Public Schools, Falmouth, MA, summer, 1968  
 Science Curriculum Supervisor - 6th grade (400 pupils, 12 teachers), Falmouth Public Schools, 1969-1970  
 Curatorial Assistant - Gray Museum, Marine Biological Laboratory, Woods Hole, MA, summer, 1974  
 Independent research (part-time, unsupported) 1960-present (supported 1965-1967) including time at sea on research vessels  
 Guest Investigator, Woods Hole Oceanographic Institution, Woods Hole, MA, 1980-present  
 Private Consultant, identification of Aplacophora molluscs, 1970-present

### **Personal**

Married, 2 grown children

### Publications

- 1963 Scheltema, R. S. and A. H. Scheltema. Pelagic larvae of New England intertidal gastropods. II. *Anachis avara*. *Hydrobiologia* 22: 85-91.
- 1965 Scheltema, R. S. and A. H. Scheltema. Pelagic larvae of New England intertidal gastropods. III. *Nassarius trivittatus*. *Hydrobiologia* 25: 321-329.
- 1965 Scheltema, A. H. Two gastropod hosts of the pyramidellid gastropod *Odostomia bisunuralis*. *Nautilus* 79: 7-10.
- 1968 Scheltema, A. H. Redescriptions of *Anachis avara* (Say) and *Anachis translirata* (Ravenel) with notes on some related species (Prosobranchia, Columbellidae). *Breviora* 304: 19 pp.
- 1969 Scheltema, A. H. Pelagic larvae of New England gastropods. IV. *Anachis translirata* and *Anachis avara* (Columbellidae, Prosobranchia). *Vie et Milieu*, Ser. A, 20: 94-104.
- 1972 Scheltema, R. S. and A. H. Scheltema. Deep-sea studies in America, 1846-1872 -- their contribution to the CHALLENGER Expedition. *Proceedings of the Royal Society of Edinburgh (B)* 72 (1971-1972): 94-104.
- 1972 Scheltema, A. H. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Z. Morph. Tiere* 72: 361-370.
- 1973 Scheltema, A. H. The radula of the Chaetodermatidae (Aplacophora, Chaetodermatida). *Proc. Fourth Eur. Malacol. Congr. Malacologia* 14: 166 (Abstract).
- 1973 Scheltema, A. H. Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Z. Morph. Tiere* 76: 97-107.
- 1976 Scheltema, A. H. Two new species of *Chaetoderma* from off West Africa (Aplacophora, Chaetodermatidae). *Journal of Molluscan Studies* 42: 223-234.
- 1976 Scheltema, A. H. and L. v. Salvini-Plawen. A giant *Neomenia* from the Magellanic Province. *Veliger* 19: 207.
- 1978 Scheltema, A. H. Position of the class Aplacophora in the phylum Mollusca. *Malacologia* 17: 99-109.
- 1981 Scheltema, A. H. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia* 20: 361-383.
- 1983 Scheltema, A. H. On some aplacophoran homologies and diets. *Malacologia* 23: 427-428.
- 1983 Scheltema, A. H. *Pinna deltodes* Menke, newly described and differentiated from *P. bicolor* Gmelin (Bivalvia, Pterioidea). *Journal of the Malacological Society of Australia* 6: 37-52.



Publications (continued)

- 1984 Scheltema, R. S. and A. H. Scheltema. Larval dispersal and the geographic range among species of the bivalve family Pinnidae. *American Zoologist* 24(3): 132A (Abstract).
- 1985 Scheltema, A. H. The genus *Prochaetoderma* (Aplacophora, Mollusca): initial account. In: L. Laubier and Cl. Monniot (eds.), *Peuplements profonds du Golfe de Gascogne*. IFREMER, Brest, pp. 391-396.
- 1985 Scheltema, A. H. The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca, Chaetodermomorpha). *Biological Bulletin* (Woods Hole) 169: 484-529.
- 1987 Scheltema, A. H. Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei*. *Marine Ecology Progress Series* 37: 171-180.
- 1988 Scheltema, A. H. Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. *American Malacological Bulletin* 6: 57-68.
- 1988 Morse, M. P. and A. H. Scheltema. Aplacophora. In: *Introduction to the study of meiofauna*, R. P. Higgins and H. Thiel (eds.). Smithsonian Press, Washington, D.C.
- 1988 Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thomson, and J. D. Williams. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. *American Fisheries Society Special Publication* 16: viii + 277.
- 1989 Scheltema, A. H. Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off southeastern Australia. *Records of the Australian Museum* 41: 47-66.
- 1989 Scheltema, A. H. Aplacophora. Chaetodermomorpha. Neomeniomorpha. In: S. P. Parker, ed., *McGraw-Hill Encyclopedia of Science and Technology*, McGraw-Hill Book Co., New York.
- 1989 Scheltema, A. H., K. Kerth, and A. M. Kuzirian. The primitive molluscan radula. *Unitas Malacologica* 10<sup>th</sup> International Congress, 27 August-2 September 1989, Tübingen, Germany. [Abstract.]
- 1990 Scheltema, A. H. Aplacophora as a Tethyan slope taxon: evidence from the Pacific. *Bulletin of Marine Science* 47: 50-61.
- 1990 Scheltema, A. H. and A. M. Kuzirian. The Aplacophora possess a true radular membrane. *American Malacological Union Annual Meeting* 3-8 June, 1990, Woods Hole, Massachusetts. [Abstract.]
- 1991 Scheltema, A. H., J. Buckland-Nicks and F.-S. Chia. *Chaetoderma argenteum* Heath, a northeastern Pacific aplacophoran mollusk redescribed (Chaetodermomorpha: Chaetodermatidae). *Veliger* 34: 204-213.

**Publications (continued)**

- 1991 Scheltema, A. H. and A. M. Kuzirian. *Helicoradomenia juani* gen. et sp. nov., a Pacific hydrothermal vent Aplacophora (Mollusca, Neomeniomorpha). *Veliger* 34: 195-203.

**In press**

Scheltema, A. H. Class Aplacophora. In: Fauna of Australia. Bureau of Flora and Fauna, Australian Dept. of Home Affairs and Environment, Canberra. (1989)

Scheltema, A. H., M. Tscherkassky and A. M. Kuzirian. Aplacophora. In: F. W. Harrison, ed., Microscopic Anatomy of Invertebrates. Wiley-Liss, Inc., New York.

**In preparation**

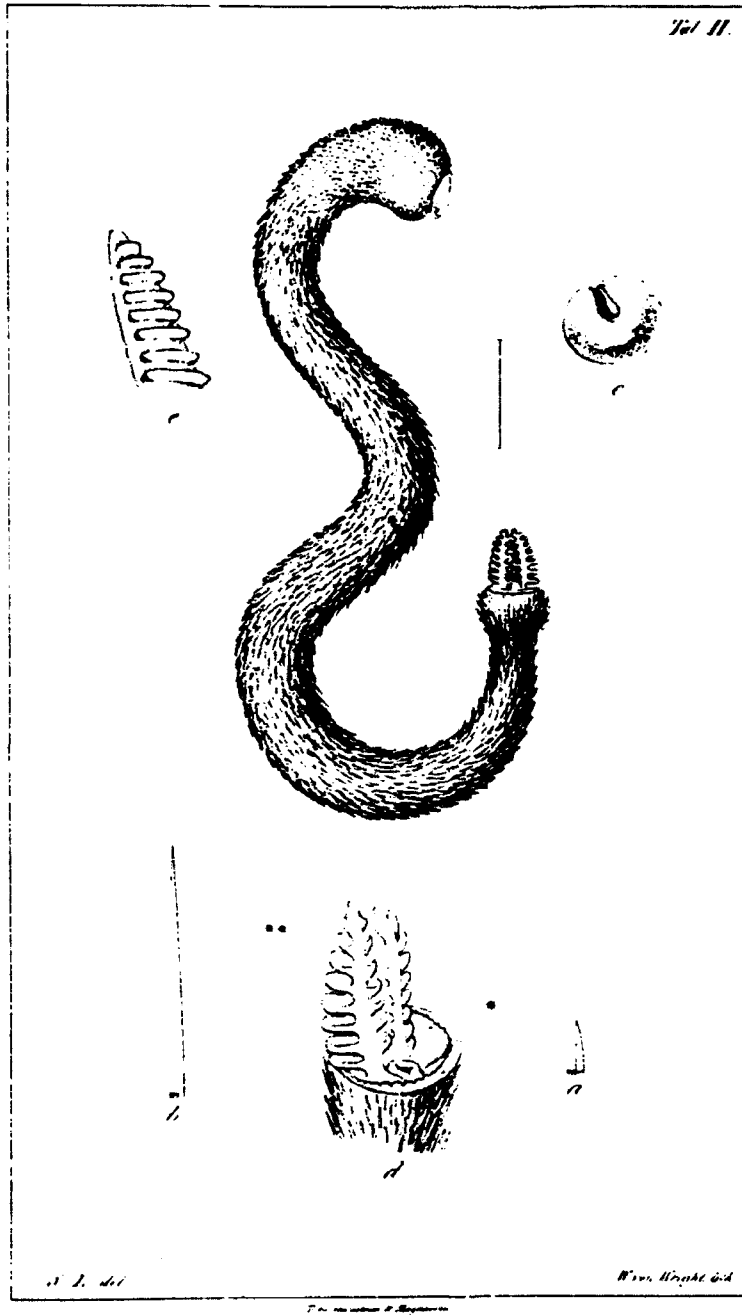
Scheltema, A. H., K. Kerth, and A. M. Kuzirian. Function and form of the primitive molluscan radula. *Malacologia*.

Scheltema, A. H. Aplacophora. In: J. A. Blake (ed.), Taxonomic Atlas of the Santa Maria [California] Basin. U.S. Department of Interior.

Scheltema, A. H. Pacific hydrothermal vent Aplacophora belonging to the genus *Helicoradomenia*.

**ILLUSTRATIONS**

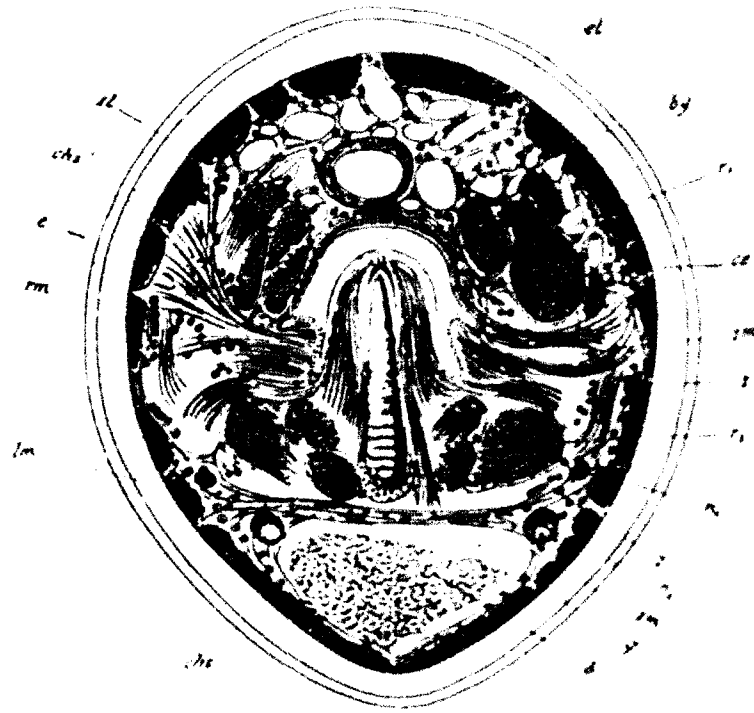
Figure 1. Copy of original drawing of *Chaetoderma nitidulum* Lovén 1844, Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar 1(4): Plate II.



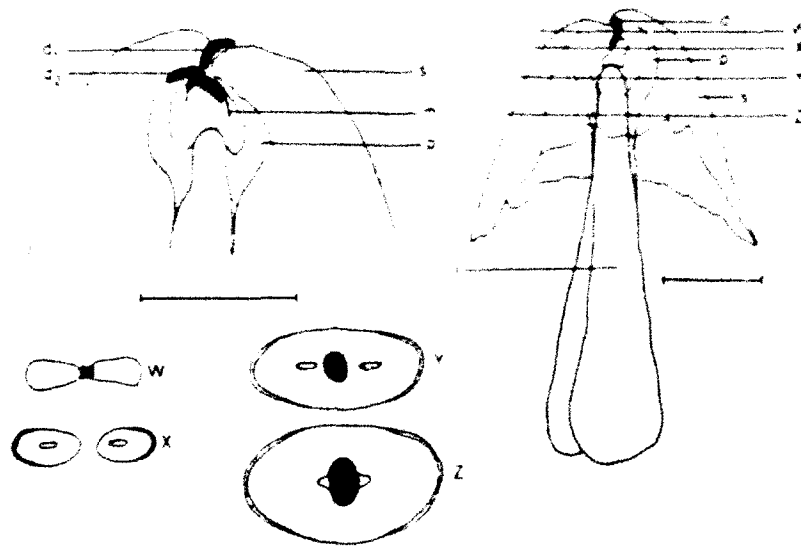
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Figure 2. *Chaetoderma nitidulum*, earliest representation of the radula showing the single cuticular cone-shaped piece (chz), paired distal denticles (zl), and cuticular dome (chz'). The bolsters are not drawn correctly. (Graff 1876 plate XI figure 4.)

Figure 3. Isolated radula of *Chaetoderma nitidulum* (from Scheltema 1972 figure 2). i = cone-shaped piece, d<sub>1</sub> d<sub>2</sub> = paired denticles, s = cuticular dome. The length of the lateral projections (p) are a useful taxonomic character (cf. Scheltema 1976 Fig. 3). Scale bars = 100  $\mu$ m.



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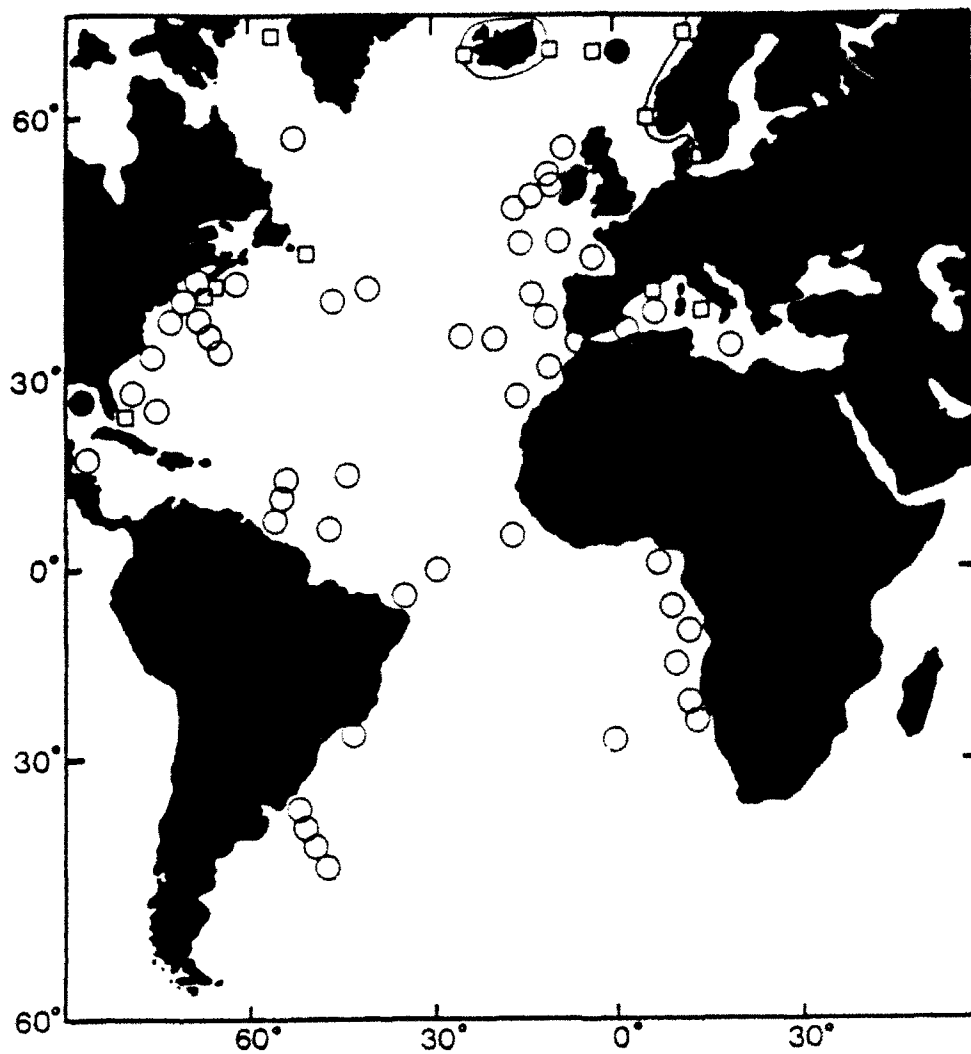


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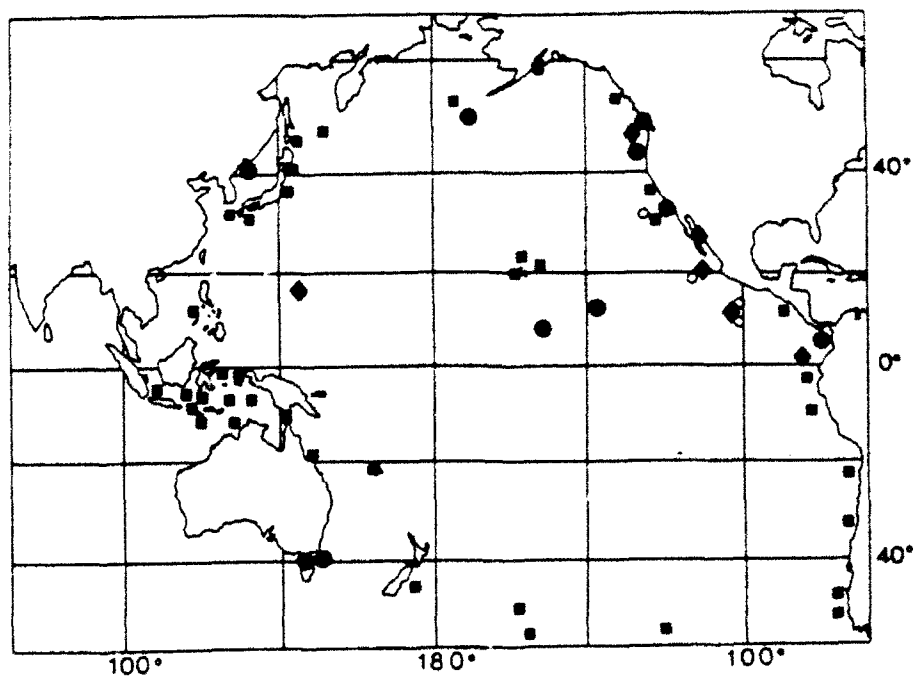
Figure 4. Aplacophora collections from the Atlantic. **Open circles**, recent collections sorted in a preliminary way by A. Scheltema (cf. Appendices C, E); **closed circles**, recent collections not sorted or not examined; **open squares**, some collections taken previous to 1960 (see text); **connecting lines** indicate area covered by sampling.

Figure 5. Aplacophora collections from the Pacific. **Large solid circles**, surveys made with an epibenthic sled or quantitative gear; **squares**, single or a few nonquantitative samples; **diamonds**, hydrothermal vent samples; **small open circles**, guyots. Material examined and sorted by A. Scheltema: **solid circles** except Sea of Japan, **open circles** and **diamonds** (cf. Appendix D). (From Scheltema 1990.)





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Figure 6. Spicules of two closely related species of *Dorymenia*, *Dorymenia* sp. (A-C, E, G) and *D. sarsii* (Kor. & Daniel.) (D, F, H), and copulatory spicules of *Simrothiella margaritacea* (Kor. & Daniel.) (J, K). Copulatory spicules of *Dorymenia* are probably deciduous: in A, a solid calcium carbonate tip extends beyond a long, twisted hyaline stem stiffened by numerous calcium carbonate crystals; in B, the stem is short and flaccid with little calcification, presumably from loss, and the tip is friable on drying. A pair of fully formed tips without stems were found in the same specimen as the fully formed spicule shown in A; presumably the tips form before the stems. The enlarged drawings of tips and accessory copulatory spicules (C, D) show clear differences between the two *Dorymenia* species. *Dorymenia* has both hollow skeletal epidermal spicules (G, H), which are similar among species, and solid, upright, curved, paddle-shaped spicules which differentiate species (E, F). In E, both frontal and side views are shown. The copulatory spicules (J) and smaller s-shaped accessory spicule (K) of *S. margaritacea* are hollow.

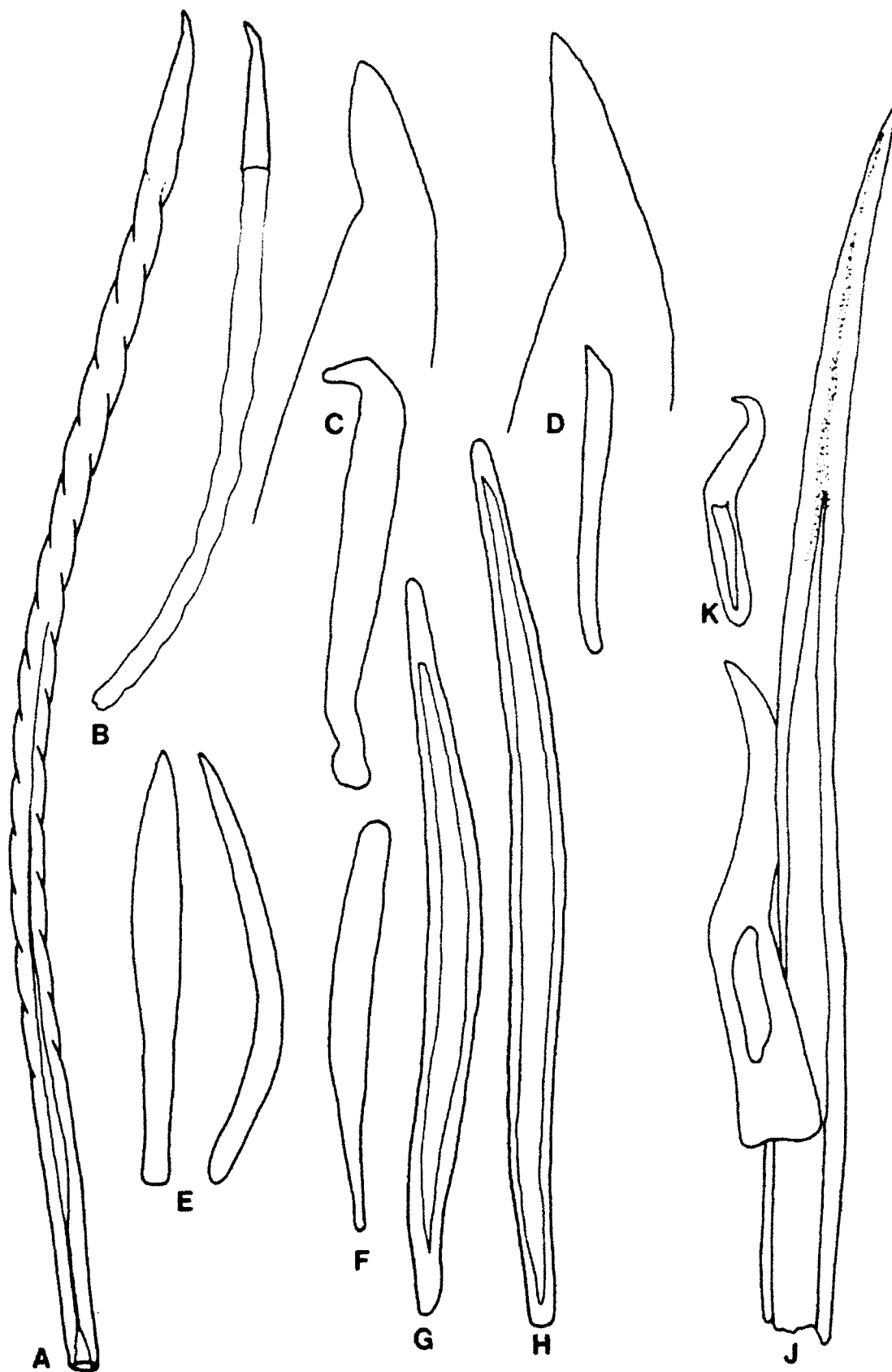


Figure 7. Spicules of two closely related species of aplacophorans under cross-polarized light. In *Chevroderma turnerae* (above) the arrowhead indicates that the thickest part of the spicule (8  $\mu\text{m}$ , third order blue for aragonite) is proximal to the narrowed waist, or lateral indentations, of the spicule. In *C. gausson* (below), the thickest part of the spicule (10  $\mu\text{m}$ , third order yellow) is distal to the waist. In both spicules the generic characters of a medial groove and asymmetry of thickening can be seen. The specimens came from the same epibenthic sled sampled (CHAIN 106 Stn. 328, 4,426 m in the European Basin off Ireland). Length of upper spicule 260  $\mu\text{m}$ , lower spicule 370  $\mu\text{m}$ .

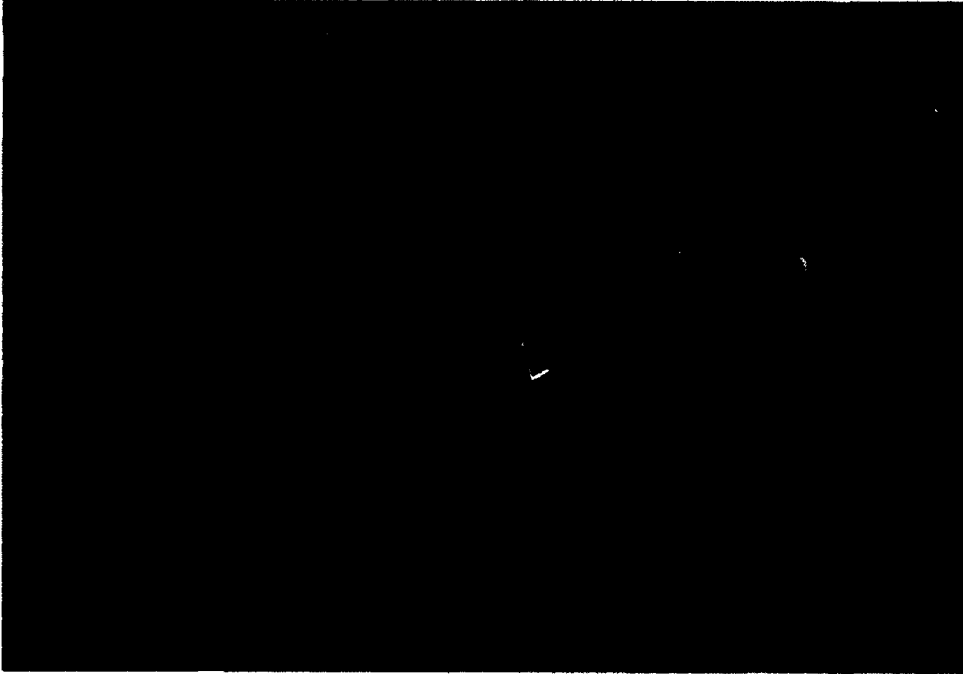


Figure 8. Radula types in Neomeniomorpha. Distichous = 2 teeth per row, monostichous = 1 tooth per row, polystichous = 4 or more teeth per row. Stippling indicates radular membrane. All drawings original except F. Scales vary.

- A. Distichous denticulate hooks. *Eleutheromenia* sp., Pararrhopalidae
- B. Distichous denticulate bars. *Helicoradomenia* sp., Simrothiellidae
- C. Modified distichous bars, oldest teeth pectinate, younger teeth denticulate. *Simrothiella margaritacea* (Kor. & Daniel.), Simrothiellidae
- D. Distichous pectinate bars. *Kruppomenia* sp., Simrothiellidae
- E. Monostichous pectinate bar. *Macellomenia* sp., Macellomeniidae
- F. Monostichous, denticles not fused. *Alexandromenia valida* Heath, Amphimeniidae (after Heath 1911 pl. 34 fig. 14)
- G. Monostichous, denticles fused. *Lyratoherpia* sp., Dondersiidae
- H. Monostichous, denticles fused. *Acanthomenia* sp., Acanthomeniidae
- J. Polystichous. *Dorymenia sarsii* (Kor. & Daniel.), Proneomeniidae (Bergen Museum No. 53025)
- K. Polystichous. *Dorymenia* sp., Proneomeniidae.

In J and K, differences in lengths of teeth numbered 1 and width of bases in teeth numbered 4 and 5 are species characters.

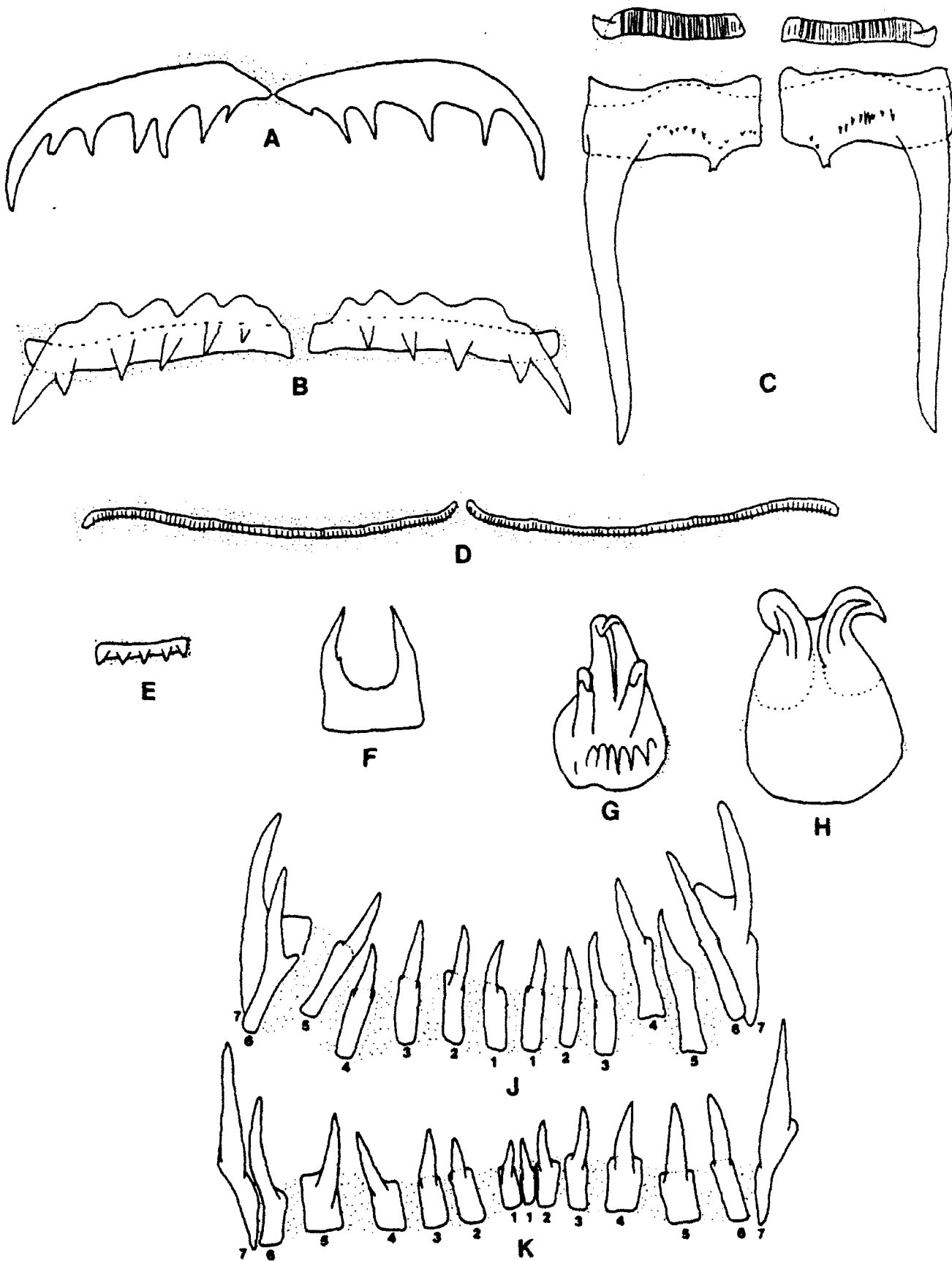
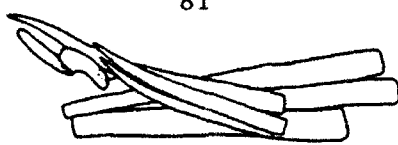
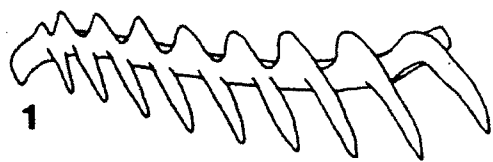
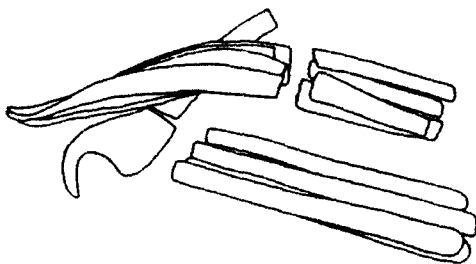
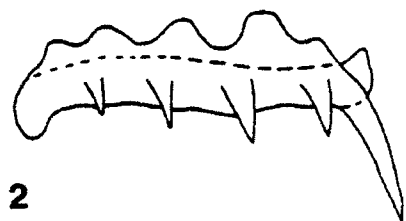


Figure 9. Spicules and radulae of 7 species of *Helicoradomenia* from Pacific hydrothermal vents. Only species 6 has been described (*H. juani* Scheltema & Kuzirian 1991). Columns from left to right: single radular tooth of distichous pair, copulatory spicules, accessory copulatory spicules if known, and epidermal spicules. The scale within each column is the same for all species but varies between columns. Evolutionary relationships among the 7 species cannot be determined by a single character: species 4-7 have similar copulatory spicules but species 4 lacks the scythe-shaped epidermal spicules of species 5-7; species 2 has similarities in copulatory spicules with species 1, but the radula is most similar to species 4-7; and species 1-4 have similar epidermal spicules but different copulatory spicules.

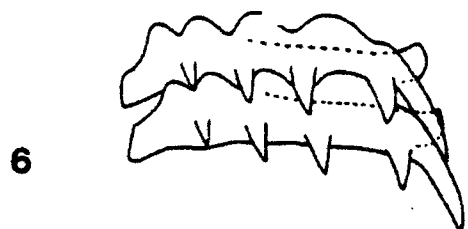
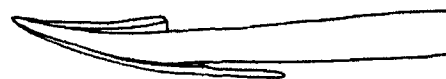
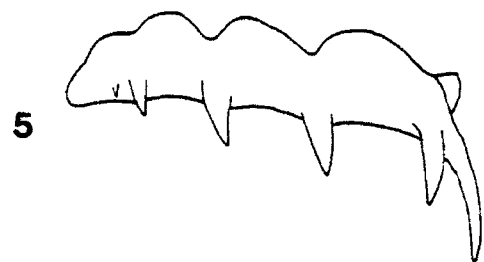
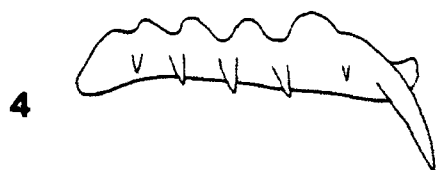
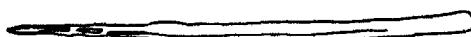
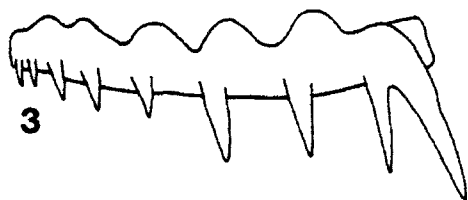
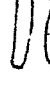
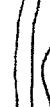
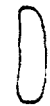




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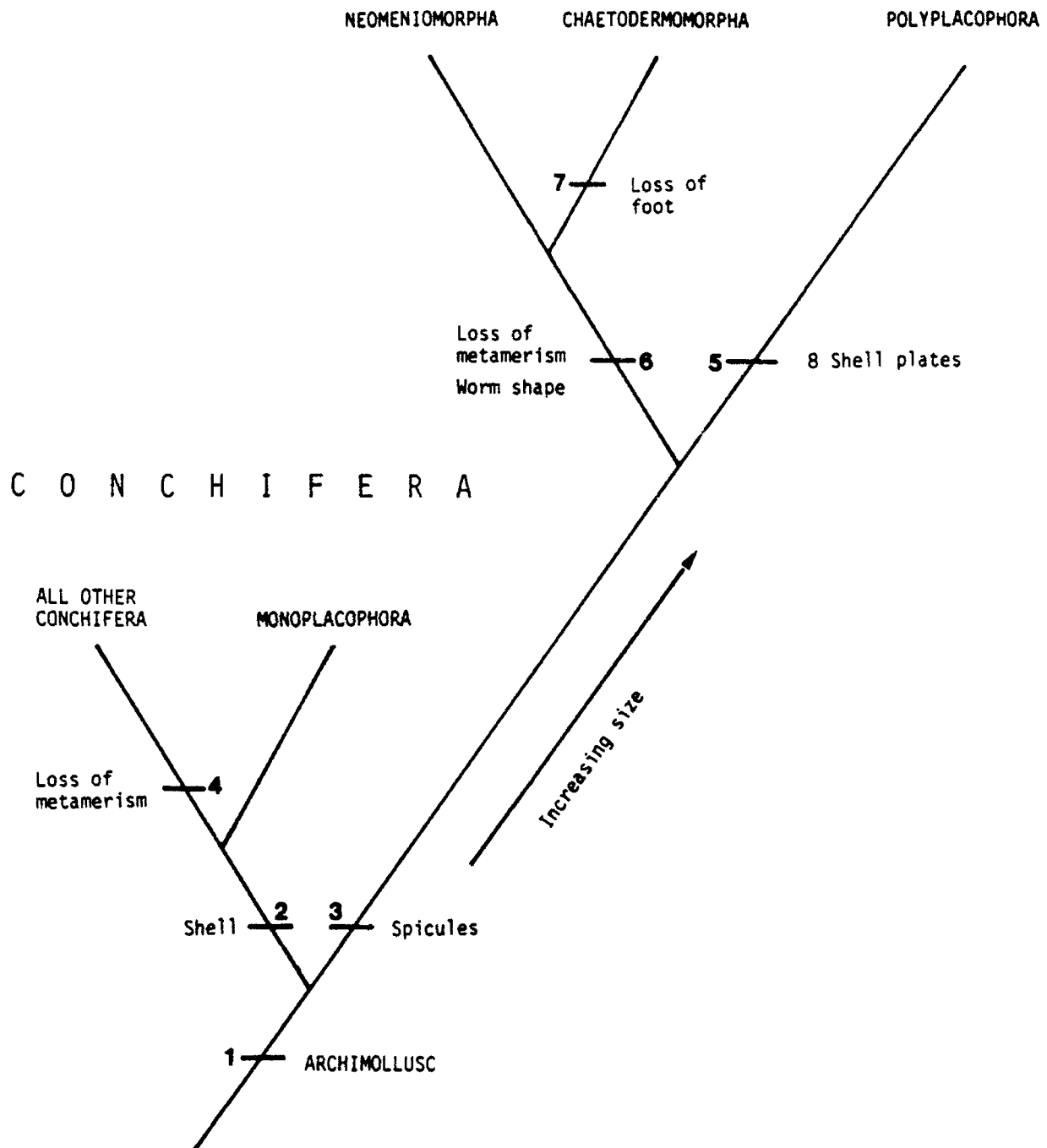
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Figure 10. A cladogram of molluscan relationships. (1) The ancestral mollusc was metameric and had a cuticle stiffened by  $\text{CaCO}_3$  but with no spicules or shell; see text for other characters. Two groups of Mollusca evolved, separated by the apomorphies of outer  $\text{CaCO}_3$  cover: (2) shell from a shell-field invagination (Conchifera) and (3) spicules (Aculifera). The Monoplacophora retained metamerism. (4) Metamery was mostly lost in all other Conchifera. (5) After an increase in size, chitons evolved with 8 shell plates. (6) Through progenesis the Aplacophora acquired a worm shape and lost metamerism. (7) The Chaetodermomorpha separated from the Neomeniomorpha with loss of the foot.

## A C U L I F E R A





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**[FLORA AND FAUNA OF AUSTRALIA]****Class Aplacophora<sup>1</sup>**

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**1. Definition and general description**

The Aplacophora are worm-shaped marine molluscs covered by a cuticle invested with innumerable calcareous spicules. Most species are small, often less than 5 mm in length, but some attain 300 mm. The head with a mouth is poorly differentiated. There is a small posterior mantle cavity. Although their shape is specialized, Aplacophora have organ systems that reflect a primitive molluscan condition in the radula, integument, gonad-pericardium, muscles, and nervous system. There are two distinct groups, the subclass Neomeniomorpha (neomenioids) with a ventral groove within which there is a narrow foot and the Chaetodermomorpha (chaetoderms) without a groove or foot and having a cuticular shield around the mouth. Aplacophora are mostly continental shelf and deep-sea forms.

In older literature the class Aplacophora is often called Solenogastres, but at present this name is applied only to the Neomeniomorpha in an alternate classification (see Classification section below; Salvini-Plawen 1967, 1972).

Ten families, 17 genera, and 33 species of continental shelf aplacophorans from off continental Australia and Macquarie Island are considered in this chapter based on the author's identifications of recently collected material, most of which is still to be published. Most of a large collection from the upper continental slope off southeastern Australia has not yet been identified and is not included here. For species of Aplacophorans off the Australian Antarctic Territories, Salvini-Plawen (1978b) should be consulted, and the area is not treated here. No Aplacophora have been reported from Lord Howe Island, Cocos (Keeling) Islands, or the Australian External Territories (Christmas, Heard, and Norfolk Islands), although a few species have been described in the region of Heard Island (Salvini-Plawen 1978b).

**2. History of discovery**

After initial discoveries in Scandinavian waters of the Chaetodermomorpha in 1844 and the Neomeniomorpha in 1875, aplacophoran specimens subsequently were recognized in collections dredged by early oceanographic expeditions prior to 1915. Species also became known from

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<sup>1</sup>Woods Hole Oceanographic Institution Contribution No. 7655.

inshore dredgings, especially in the vicinities of European marine research stations. It was not until the early 1960s that improved equipment and sieving techniques, combined with systematic sampling, first provided adequate representation of continental shelf and deep-sea macro-infauna populations (Sanders *et al.* 1965). Aplacophorans are now known to form a numerically small but consistent element of the deep-sea fauna (Gage and Tyler 1991), but particular species are sometimes numerically dominant in quantitative samples (Scheltema 1985). Recent studies on the inshore meiofauna (small interstitial animals) have shown that aplacophorans often occur as part of the psammon (sand meiofauna) (Morse 1979, Salvini-Plawen 1985a).

Five late 19<sup>th</sup> and early 20<sup>th</sup> century expeditions that dredged in Australian waters, or collected Pacific and Indian Ocean aplacophoran species or genera that may also occur off Australia, are: *Challenger* (Selenka 1885: 1 species, Philippines); *Gazelle* (Thiele 1897, 1902a: 3 species, northwest coast Australia, Torres Strait, Banda Sea); *Valdivia* (Thiele 1902b, 1906: 2 species, off east and south Africa); *Siboga* (Nierstrasz 1902, Stork 1941: 14 species excluding synonyms, East Indies), and *Albatross* (Heath 1911: 12 species, Hawaiian Islands and southern Japan). Other aplacophorans from the western Pacific and Indian Oceans have been described by Baba (1940a: 1 species, southern Japan); Salvini-Plawen (1969: 2 species, Red Sea; 1978b: 1 species, Macquarie Island, 1988a: 1 species, Bass Strait); Ponder (1970: 1 species, Chatham Island, New Zealand); and Ivanov (1984: 4 species, Sea of Japan).

Except for two species of Neomeniomorpha reported nearly a century ago from off northern Australia (*Epimenia australis*, *Notomenia clavigera*, Thiele 1897, 1902), no further aplacophorans were collected from Australian waters until recently. Since 1975 surveys have been made on the shelf of the Great Barrier Reef (2 species), Macquarie Island (1 species), Bass Strait (28 species), and the continental slope off southeast Australia (about 40 species). Although most await description, five species of Chaetodermomorpha from the slope and shelf have been published (Scheltema 1989), the first of this subclass to be reported from Australia (*Falcidens chiastos*, *F. lipuros*, *F. macrafrondis*, *Chaetoderma usitatum*, *Rhabdoderma australe*). One other Australian aplacophoran has been described, *Dorymenia harpagata*, from Macquarie Island (Salvini-Plawen 1978b).

### 3. Morphology and physiology

A general description of the Aplacophora is found in Salvini-Plawen and a description of the microscopic anatomy is found in Scheltema *et al.* (in press).

#### 3.1 External features and spicules

The shape of aplacophorans varies considerably from nearly spherical to elongate and slender but shape is usually consistent within families or genera. In cross-section Chaetodermomorpha are round whereas Neomeniomorpha may be round, or low and broad, or narrow and high, or triangular, or dorsally carinate, bicarinate, or tricarinate. The spicular covering varies from smooth to very spiny.

The undifferentiated head has a terminal or subterminal mouth opening. The opening of the small posterior mantle cavity is defined by a terminal circular ridge of spines in chaetoderms and often by a brush of subterminal spines in neomenioids. The neomenioid foot is formed by a simple, non-muscular, ciliated fold or folds and is hidden within the ventral longitudinal groove in preserved specimens.



The epidermis produces the cuticle and spicules. The cuticle of *Rhopalomenia* is considered to be an early mucoid stage in the evolution of molluscan shell (Beedham and Trueman 1968). In *Chevroderma* the cuticle is fibrous (Scheltema 1985).

As in the Polyplacophora each spicule is secreted extracellularly (Haas 1981). It starts within an invagination of an individual cell and grows out through the cuticle. A collar of neighboring cells seals off the crystallization chamber. The spicules in all species examined are aragonitic except in the Notomeniidae, which lack calcium carbonate. Spicule morphology varies greatly from flattened and leaf-like in chaetoderms and some neomenioids to paddle- or hook-shaped or rounded and needle-like in other neomenioids. There may be slight to elaborate ornamentation on the spicules of the Chaetodermomorpha and in many Neomeniomorpha the spicules are hollow. There are one to several forms of spicules on a specimen; the forms are species-specific and may be restricted to particular regions of the body.

### 3.2 Musculature

Four muscle layers, not always fully expressed, lie beneath the epidermis: an outer circular layer, an inner longitudinal layer, and between them, two oblique layers at right angles to each other. Neomeniomorpha also have two ventral bands of thickened longitudinal muscles, giving many species in this taxon a typical flexed new-moon shape. In the chaetoderms (except *Limifossor*) the longitudinal muscles separate into four distinct bands which either run throughout the body length or are restricted to anterior or posterior regions. Posteriorly the longitudinal muscles of the body wall give off bands or fibers that retract the ctenidia (chaetoderms) or respiratory folds (neomenioids) of the mantle cavity and anteriorly the longitudinal muscles give off bands that move the head. Internal organs are attached by fine strands to the body-wall. In most neomenioids there are series of lateroventral muscles that produce sacs of the midgut.

### 3.3 Body cavities

Most of the internal space of aplacophorans not occupied by muscles and organs is haemocoel, divided by a fine ventral muscular horizontal septum to produce a pedal sinus (Fig. 1A). Transverse septa may be present near the anterior or posterior ends. Coelomic spaces are restricted to the posterior pericardium, which is large relative to the size of the heart (Scheltema 1973, 1988), and to the reproductive organs -- gonads and gametoducts.

### 3.4 Feeding and digestion

All Aplacophora insofar as is known are either carnivores or selective detritivores. The Neomeniomorpha feed on Cnidaria; the Chaetodermomorpha eat small organisms and organic detritus (Salvini-Plawen 1981; Scheltema 1981). Chaetoderms and most neomenioids, like other molluscs, have a discrete buccal mass with a radula, radular sac, and paired or fused bolsters with their protractor and retractor muscles (Fig. 1). Jaws are lacking except in the Prochaetodermatidae. The most generalized radula is distichous, with rows of two opposed, mirror-image, denticulate teeth on a unipartite or bipartite radular membrane (Fig. 13C). A central tooth is lacking except in the Prochaetodermatidae which have a medial flat plate (Scheltema 1981, 1988). Radulae vary morphologically and several neomenioids have no radula. The teeth are produced by odontoblasts at the proximal end of a radular sac and decrease in size from newest to oldest. Denticle number can vary both within and between rows of a single

radula (Fig. 11C, 12C). The paired bolsters are often chondroid-like in cell structure (Scheltema 1981, Scheltema *et al.* in press).

The radula apparently does not function as a rasping organ except in the Prochaetodermatidae, the only taxon in which distal teeth show wear (Scheltema 1981). Feeding has not been observed in any aplacophoran, and the use of the radula is only inferred from its position in fixed material (e.g. Heath 1911) or movements in living specimens (e.g. Baba 1940b; Salvini-Plawen 1981).

The foregut consists of a mouth, an oral cavity, a pharynx into which salivary glands open and which contains the radula and sometimes an esophagus. The midgut has a simple stomach either united with a digestive gland in neomenioids or separate from a sac-like digestive gland in chaetoderms. The hindgut is formed of a long or short intestine that bends ventrally to empty posteriorly through an anus into the mantle cavity.

### 3.5 Circulation

A heart consisting of a ventricle and (usually) paired auricles lies posteriorly within the pericardium (Fig. 1). Blood either passes forward from the heart through a dorsal aorta that empties near the cerebral ganglion, or the heart empties directly into the dorsal haemocoel. The remainder of the circulation is open, with blood moving freely through the haemocoel and its sinuses by movements of the body. There are three types of blood cells: erythrocytes, amoebocytes, and platelets. Five pairs of closely related species of Proneomeniidae in the Antarctic and sub-Antarctic differ from each other in form of erythrocyte (Salvini-Plawen 1978a). Phagocytosis by the amoebocytes has been demonstrated only in the Epimeniidae (Baba 1940b). Heartbeat has been observed to be between 19 and 42 beats per minute (Salvini-Plawen 1968a, 1968b).

### 3.6 Excretion

Excretion seems to occur in at least two ways. Phagocytized material was shown experimentally to pass directly into the midgut in the Epimeniidae and thence was expelled into the mantle cavity (Baba 1940b). No other experimental results have been published. However, nearly all aplacophorans have epidermal cells or papillae that are filled with granular material and that in histologic sections appear to discharge to the outside through the cuticle. If the cuticle is thick, the papillae are stalked (Hoffman 1949). Whether the ctenidia, mantle cavity folds, or the gametoducts function in excretion is not known. Kidneys are lacking.

### 3.7 Respiration

There are paired ctenidia in the mantle cavity of chaetoderms and simple mantle-wall folds or papillae in neomenioids (Fig. 1). Blood cells have been observed to circulate in both (Pruvot 1891; Salvini-Plawen 1968a) and they are assumed to serve in respiration, but there are no experimental or fine-structure studies to substantiate the assumption.

### 3.8 Sense organs and nervous system

The nervous system is ladderlike (Heath 1904, 1911; Hyman 1967; Salvini-Plawen 1985b). Two pairs of ganglionated nerve cords, a lateral and a ventral, arise separately or from a common root from a large, bilobed anterodorsal cerebral ganglion and run the length of the

body (Figs. 1, 2). The lateral cords end in a posterior suprarectal commissure, sometimes greatly enlarged in the chaetoderms. Several pairs of nerves more or less swollen at their bases arise frontally from the cerebral ganglion to innervate the mouth and sensory vestibule (neomenioids) or oral shield (chaetoderms). On each side cross-commissures run between the lateral and ventral cords, and ventrally they run between the ventral cords. The latter are more numerous in the footed neomenioids than in the chaetoderms. The lateral cords contribute nerves to the body wall and internal organs. In the chaetoderms they descend and run parallel to the ventral cords fusing with them posteriorly. A pair of buccal connectives arise from the cerebral ganglion or the common roots of the longitudinal nerve cords and run to a pair of buccal ganglia connected by one or two commissures in the region of the radula. There may also be pharyngeal ganglia and nerve rings. Posteriorly the suprarectal commissure gives off a single nerve or a pair of nerves to a dorsal sensory organ (Salvini-Plawen 1972, 1985b).

The function of sensory organs in the Aplacophora is not known. The posterior dorsal sensory organ is usually present. It is protrusible and may function in reproductive behaviour (Haszprunar 1987). Some neomenioids have additional sensory pits on the body surface. The vestibule of neomenioids, located dorso-anterior to the mouth, is lavishly provided with papillae and a nerve plexus. It is protruded hydrostatically and bears large, stiff cilia around a sensory rim (Pruvot 1891; Salvini-Plawen 1968b; Haszprunar 1986). It may function in food detection. The innervated oral shield of chaetoderms may serve in food detection as well as in burrowing. Statocyst-like sacs have been found anteroventrally in genera of *Gymnomeniidae* but not in other families (Salvini-Plawen 1967, 1988a; Scheltema 1981).

### 3.9 Reproduction

The Chaetodermomorpha are dioecious, whereas Neomeniomorpha are hermaphroditic. In both subclasses the paired gonads, often fused in adult chaetoderms, lie dorsally and run the length of the midgut (neomenioids) or digestive gland (chaetoderms) (Fig. 1). The gonads empty directly through (usually) paired gonopericardial ducts into the anterior end of the pericardium. Eggs or sperm are often seen to fill the pericardium in sectioned material. In the usual case, paired U-shaped gametoducts (also called in the literature gonaducts; coelomoducts; pericardioducts plus spawning ducts or shell glands) run from the pericardium to the mantle cavity. The upper gametoducts leave from the ventral, posterior end of the pericardium and turn anteriorly toward the anterior end of the pericardium. They then bend ventrally to join the lower gametoducts, which run posteriorly and open through paired gametopores (also called coelomopores), or, in most neomenioids, through a single gametopore.

The Chaetodermomorpha have a simple type of sperm which suggests that they spawn their gonadal products into the sea (Franzén 1955; Buckland-Nicks and Chia 1989). The Neomeniomorpha have a slightly modified sperm (Scheltema *et al* in press), copulatory spicules, and usually seminal receptacles and thus probably copulate, although there are no observations of pairing. The egg masses in chaetoderms are not known. In neomenioids fertilized eggs are spawned either singly or in mucous ribbons, or sometimes brooded (Pruvot 1890; Baba 1940c; Heath 1918; Salvini-Plawen 1978b).

### 3.10 Embryology and Regeneration

Hadfield (1979) and Salvini-Plawen (1985b) have reviewed the published works on reproduction and embryology in the Aplacophora. Development has been observed in a few species of Neomeniomorpha, although complete ontogeny is still unknown. Nothing has been published on the embryology of the Chaetodermomorpha. Brooding is reported in the neomenioid family Pararrhopalidae from histologic preparations. Observations on living material is restricted to four species in four genera [*Epimenia* (Baba 1938, 1940c, 1951); *Nematomenia* (Pruvot 1890); *Rhopalomenia* (Pruvot 1892); and *Neomenia* (Thompson 1960)]. Early cleavage stages have been best described in *Epimenia* (Baba 1940c) in which cleavage is spiral and unequal. Gastrulation in different species has been described as being by epiboly (Pruvot 1890), by delamination (Heath 1918), and by invagination (Baba 1940c). In *Epimenia*, which sometimes broods its larvae for part of their development, embryogenesis differs from that in the other three neomenioids in the formation of a blastopore. In the species which do not brood there is an abapical pseudoblastopore which is the precursor to the definitive ectoderm, while the rest of the outer cell layer of the gastrula forms a ciliated larval test that has an apical tuft and equatorial prototroch (Fig. 3). The number of cells that form the larval test is constant (Thompson 1960). A mass of cells within the test forms the endoderm and mesoderm. The larva, called a pericalymma, swims but does not feed and is similar to that found among the protobranch bivalves. Stomadeal and proctodeal invaginations of the definitive ectoderm form the foregut and mantle cavity; the solid endodermal mass differentiates into midgut and intestine; and mesoderm, differentiated from the internal cell mass, gives rise to muscles, and later the heart and pericardium. The only adult tissue derived from the larval test is part of the nervous system, which develops from inward proliferation of test cells. Genesis of the reproductive system has not been described, although there is some evidence that the upper gametoduct is coelomic, derived from the pericardium, and the lower gametoduct is ectodermal, derived from the mantle cavity (Baba 1940b; Salvini-Plawen 1972). Metamorphosis occurs gradually in 1 to 10 days, according to species, either by casting off larval structures or by engulfing the larval test with the proliferating ectoderm. At no stage has metamerism been observed.

*Epimenia verrucosa* held alive in the laboratory was able to regenerate the posterior end and its contained organs when extirpated (Baba 1940b).

### 4. Natural history

Little is known about the life history or ecology of Aplacophora. Experimental boxes of azoic mud placed at 2,000 m in the northwest Atlantic slope were colonized by a *Prochaetoderma* species. From boxes recovered after 2, 6, 8 and 12 months, and from measurements of individuals and of egg sizes from large epibenthic sled samples, *P. yongei* is inferred to grow to adult size in two months and to sexual maturity in one year (Scheltema, 1987). Longevity and fecundity are unknown for any species. Length-frequency measurements of large samples ( $N > 25$ ) of several species show a normal curve, which indicates low recruitment.

Aplacophora are slow-moving creatures, sometimes nearly inert. The Chaetodermomorpha are burrowers. The Neomeniomorpha are creepers either on the bottom or on the corals and hydroids upon which they feed.

Changes in the distribution of certain species over time reflect alteration in the physical environment of a region, e.g., *Chaetoderma argenteum* once common in Monterey Bay, California, USA a century ago has been replaced by another species of *Falcidens*, probably owing to an increase in temperature, the result of El Niño.

Stenotopy is inferred in the Chaetodermatidae. *Chaetoderma nitidulum canadense* from Cape Cod Bay, Massachusetts, USA, is restricted to temperatures of less than 10°C and to sediments with not more than 20% clay (author's unpublished data).

## 5. Biogeography

The Australian aplacophoran fauna of the continental shelf is the consequence of several influences. Some genera in both subclasses reflect an ancient Tethyan distribution, occurring in the Mediterranean, eastern and western Atlantic, and southeastern Australia, but not in the eastern Pacific, insofar as known (Scheltema 1990). Examples are *Pararrhopalia*, *Eleutheromenia*, and a particular *Falcidens* group that has spicules with diagonally crossed ridges (Figs. 4D, \_\_\_B). Two genera found in Bass Strait, *Nematomenia* and *Neomenia*, have a worldwide distribution, and one tropical Indo-Pacific genus, *Epimenia*, was collected on the shelf off northwest Australia. Antarctic affinities are indicated by the Phyllomeniidae in Bass Strait and the genus *Ocheyoherpia* from Macquarie Island.

Endemicity of genera to Australia appears to be limited to three: one new genus in the Pararrhopalidae, one new genus placed provisionally in the Phyllomeniidae, and *Notomenia* in the unique monogeneric family Notomeniidae. Lack of endemicity at shelf depths may be due to colonization from a Tethyan fauna at upper slope depths, where aplacophorans worldwide reach their greatest numbers and diversity (Scheltema 1990). Endemicity at the species level cannot yet be determined because the Pacific aplacophoran fauna is too poorly known. However, the radiation expressed by very closely related species within genera of the neomenioid families Pararrhopalidae and Lepidomeniidae and in the chaetoderm genus *Falcidens* suggests that species endemicity may be high in southern Australia.

The aplacophoran shelf fauna of the Bass Strait area of southern Australia is one of the most diverse known, with 32 species in 9 or 10 families and 13 to 15 genera. Three hundred seventy-six specimens have been collected at 32 localities. The two subclasses are about equally represented in number of specimens but are very different in diversity. The Chaetodermomorpha represent two families, two or three genera, and four species, but 98% of chaetoderm specimens belong to a single species, *Falcidens chiastos*. There are 28 species of neomenioids in 11 or 12 genera and seven or eight families. Numbers of one new pararrhopalid species of *Eleutheromenia* are high, accounting for 30% of all neomenioids collected.

Species at depths less than 125 m in Bass Strait appear to be limited to the continental shelf, whereas some species occurring at 140 m have also been collected from the upper slope.

Besides the Bass Strait region, the only other shelf area in Australia that has been systematically sampled using fine screens is Cleveland and Halifax Bays, North Queensland. Only a few specimens limited to two species (not described) have been collected, one in the Lepidomeniidae and the other in the Pararrhopalidae.

Two taxa that are commonly found on continental shelves in other parts of the world are missing from the shelf off continental Australia: the neomenioid family Proneomeniidae and the chaetoderm genus *Chaetoderma* (Scheltema 1989 and author's unpublished data). However, both

taxa are found on the slope below 200 m, and a species of *Proneomeniidae* has been recorded from shelf depths off Macquarie Island (Salvini-Plawen 1978b).

## 6. Fossil history

Fossil Aplacophora are not known. However, spicules and radulae could be preserved under particular circumstances.

## 7. Methods of study

Hard parts -- spicules and radulae -- and external characters such as overall shape, spicule attitude and arrangement, and shape of anterior and posterior ends, can be utilized in taxonomic studies. New species of *Neomeniomorpha* require histologic preparations to determine higher classification. Aplacophoran specimens should be preserved in relatively large volumes of buffered 80% EtOH to preserve spicules. Inadequate preservation can denude specimens of spicules. Permanent slides of holotype spicules should be prepared. See subclass headings for preparation techniques.

Most aplacophorans have been collected with dredges, box cores, or grabs. The entire contents of such a sample should be sieved through a 0.5-mm screen using a flotation method (Sanders et al. 1965), fixed for 24 hours in buffered formalin, and then preserved in 80% buffered alcohol. The addition of rose bengal to a sample prior to sorting differentiates organisms collected alive from detritus.

Interstitial aplacophorans can be captured by collecting coarse sand subject to swift currents or wave action (1) by dredging with a canvas-lined anchor dredge; (2) by divers using buckets or suction guns; or (3) intertidally with a spade from around boulders where tidal amplitudes are greater than 8 m (Morse and Scheltema 1988). Moist sand is left standing in tubs for up to several days. Surface sand is then subsampled into a small bucket. Sea water is added with vigorous stirring and rapidly decanted through a 42  $\mu$ m mesh screen. The retained organisms are washed into a dish for examination under a dissecting microscope.

## 8. Classification

Two classifications are currently in use. In one the two aplacophoran groups are placed in separate classes, the *Solenogastres* and *Caudofoveata*, because their worm shape is argued to have evolved as two separate events (Salvini-Plawen 1972, 1985b). However, the worm shape of the Aplacophora is here considered to be an autapomorphy, that is, a shared, derived character arising from a single evolutionary event unique to the Aplacophora, and the two groups of Aplacophora are placed as the subclasses *Neomeniomorpha* and *Chaetodermomorpha* in a single Class (Scheltema 1978, 1988; Scheltema and Kuzirian 1991). Historically, the first two aplacophoran species to be described were *Chaetoderma nitidulum* Lovén 1844 and *Neomenia carinata* Tullberg 1875, which gave their names to the two aplacophoran taxa that are retained here.

Class Aplacophora Ihering 1876 [= *Solenogastres* Gegenbaur 1878]

Subclass Chaetodermomorpha Pelseneer 1906 [= *Caudofoveata* Boettger 1956]

Subclass Neomeniomorpha Pelseneer 1906 [= *Ventroplicida* Boettger 1956;

Class *Solenogastres* Gegenbaur 1878 (partim), sensu nomine Salvini-Plawen 1967]

The Neomeniomorpha have been divided into four orders (Salvini-Plawen 1978b; Boss 1982), but because certain characters described here under family headings cross ordinal boundaries (e.g. Pararrhopalidae), these orders are considered polyphyletic and are not maintained (see also Salvini-Plawen 1978b p. 24, Cavibelonia; Scheltema and Kuzirian 1991).

### Key to the subclasses of Aplacophora

1. (a) Ventral furrow absent, oral shield present.....Chaetodermomorpha
- (b) Ventral furrow present, oral shield absent.....Neomeniomorpha

### Subclass Chaetodermomorpha

The burrowing chaetoderms are recognized by their cuticular oral shield (Figs. 4B, 5A) and lack of a ventral furrow and foot. They are placed into family by shape, by the way the spicules are born in the cuticle, and by radula morphology. There are three named families with 10 genera and 83 species worldwide.

The first members of this subclass were collected only recently from the benthos off Australia. Although all families and six genera of Chaetodermomorpha occur on the continental slope off southeastern Australia, only two families with two or three genera occur in the collections from the shelf and only from Bass Strait. The shelf Prochaetodermatidae are represented by a single decalcified specimen belonging to an undetermined genus, and one specimen of another species probably belonging to the Chaetodermatidae awaits generic determination. All other 202 chaetoderm specimens collected from the shelf belong to two species of *Falcidens*, one represented by only three specimens.

Spicules extend for part or most of their length beyond the cuticle and are held either flat against the body or raised slightly or perpendicularly to the body; both flat and raised spicules may occur on the same specimen. Some species have flat-lying spicules mostly embedded in the cuticle. All spicules except those held vertically are imbricated, overlapping like shingles. Spicules are oriented either anteriorly-posteriorly parallel to the mid-body axis (Fig. 4) or anteroventrally-dorsoposteriorly at an angle to the axis (Fig. 5). Sculpture of the spicule usually runs as lengthwise ridges and grooves and presumably helps maintain spicule orientation as the animal expands and contracts while in motion. An exception to lengthwise sculpture is found in the Australian species *Falcidens chiastos* (Fig. 4D).

The placement of four heavy longitudinal muscle bands defines body shape. In *Scutopus* and some Chaetodermatidae, these muscles run the length of the body, and the body is of nearly equal width throughout. In most Chaetodermatidae the longitudinal muscle bands are thickest either anteriorly, and the posterior part of the body is widest (Fig. 4A), or they are thickest posteriorly, that end then being narrowest and "tail-like". In the Prochaetodermatidae, the thickest muscle bands are posterior and the species are all "tailed". (Fig. 5A). An anterior constriction of the body sets off a "neck" in the Chaetodermatidae and *Scutopus*, the site of attachment for muscles running anteriorly which move the anterior end. Measurements of body regions as defined by muscle bands are important taxonomic characters (Scheltema 1976, 1985, 1989).

Burrowing is slow, complete burial within the substrate from the surface measured in hours

rather than minutes (personal observation). It is brought about by pushing the anterior end by means of hydrostatic pressure into the sediment. The ring of usually long, needle-like spicules around the mantle cavity act as an anchor while the anterior end is moved forward. The heavy longitudinal muscles then contract to bring the rest of the body forward (Wirén 1892a; Salvini-Plawen 1985b). The anterior end of chaetodermatid species is capable of turning through nearly 360° around the long axis of the body and of moving dorsally to ventrally through about 180°. The oral shield, with mucous cells opening beside and through it, thus becomes an effective shovel (Scheltema *et al.* in press).

The radula varies widely: it is distichous, with two teeth per row on a radular membrane, or it is specialized. In the Prochaetodermatidae, the radula has evolved into a rasping organ with distichous teeth and a central plate reminiscent in morphology to that of many gastropods (Scheltema 1981). From fixed specimens, prochaetodermatids are seen to feed by ingesting large clumps of organic matter, foraminifera, or other organisms into an expandable pharynx where the food is held between large cuticular jaws. The teeth then rasp this material (original observation; manner of feeding stated incorrectly, Scheltema 1981). In Chaetodermatidae, the radula consists of a large cone with two small distal denticles (Scheltema 1972) (Fig. 4C, F). This radular apparatus may work as a transport device (Ivanov 1979) or as pincers to grab the organisms upon which chaetodermatids feed. Particular muscles of the various radular types among families are homologous (Deimel 1982). The pharynx passes directly into the stomach, or into a postradular, tubular esophagus (Fig. 1A). The stomach varies in length from short to more than half the body length. In the Chaetodermatidae, but not in other families of the subclass, a gastric shield is found at the posterior end of the stomach at the point where the digestive gland opens into it. At the same level, a mucoid rod projects from a ciliated style-like sac of the intestine where it joins the stomach (Scheltema 1978, 1981). Because the Chaetodermatidae is a more specialized group within the subclass, this gastric shield is considered to be analogous, but not homologous, to the gastric shield in other Mollusca. The digestive gland is a large, blind sac that fills most of the posterior part of the body except the "tail" if present. Dorsally the sac is lined with cells filled with coarse yellow granules (lacking in the Prochaetodermatidae). Laterally and ventrally the cells secrete large basophilic spheres (mostly eosinophilic in the Prochaetodermatidae) (Scheltema 1981; Salvini-Plawen 1988b; Scheltema *et al.* in press). From histologic evidence digestion is said to be extracellular (Salvini-Plawen 1988b). The intestine is long, running from the stomach dorsolaterally along the digestive gland and gonad. It bends ventrally to open into the mantle cavity between the ctenidia.

Besides probable excretion from integumental papillae, there is evidence of excretion from the mantle cavity, the outside wall of which is often lightly to heavily encrusted with a yellow deposit.

The paired ctenidia in the mantle cavity are often very large and in their form are typical for molluscs. In life they extend beyond the opened mantle cavity, and elongate lateral cilia of the ctenidial folds pass water from the dorsal to ventral surfaces between the leaves of the gill (Salvini-Plawen 1985b). An afferent membrane attaches the ctenidium ventrolaterally to the mantle wall. A shorter efferent membrane is dorsal.

The gonads are paired or fused and lie in the posterior part of the body anterior to the "tail" if this is present. The length of the gonopericardial ducts are short or long, depending on whether there is a "tail." The gametoducts are without elaboration and open separately into the mantle cavity. The male gametopore may be on a muscular papilla. The female gametopore opens onto a tract of mucous cells that may secrete a substance to bind emerging eggs into a



mass. There are no copulatory spicules. Animals in Scandinavia are reported to be ripe in the fall and winter (Salvini-Plawen 1985b).

Taxonomic characters used for the identification and classification of Chaetodermomorpha are (a) the morphology of the spicules and radula, (b) the absolute and relative measurements of body regions and oral shield, and (c) arrangement of the spicules along the body and around the mantle cavity (see e.g. Scheltema 1976, 1985, 1989; Salvini-Plawen 1967, 1969). Spicules may be teased from specific regions of the body after placing the animal in a drop of glycerine in a depression slide. The buccal mass can be dissected out after making a longitudinal dorsal cut at the anterior end and the radula freed from the tissue by using hypochlorite or KOH solutions. For study the radula is then placed in glycerine after rinsing with distilled water. Body measurements are made by drawing a line along the midline of a camera-lucida image. Each region is demarcated, and a line perpendicular to the midline is drawn within each region in order to derive a measurement of the diameter. The lines can be measured by using calipers, a map-measuring wheel, or a digitizer. Permanent slides can be made of spicules by teasing them from a specimen directly onto a slide, air-drying, and covering with a mounting medium and coverslip. To make permanent slides of isolated radulae, they are rinsed free of glycerine and hypochlorite and mounted in CMC-10, which is miscible with water. The use of a micropipetter facilitates transfer of tiny radulae.

#### Key to the families of Australian continental shelf Chaetodermomorpha

1. (a) With oral shield entire (Fig. 4B) and four body regions  
(Fig. 4A, E) . . . . . Chaetodermatidae
- (b) With divided oral shield (Fig. 5A)  
and tail-like posterium (Fig. 5B). . . . . Prochaetodermatidae

#### Family Chaetodermatidae

The family is distinguished by having four distinct body regions: (1) the anterior neck set off by a usually distinct constriction; (2) the anterior trunk containing the stomach; (3) the posterior trunk with digestive gland and gonad; and (4) the posterium which may be short or tail-like. The oral shield is undivided. The radula is specialized with 2 small denticles at the end of a large cuticular cone (Salvini-Plawen 1968a; Scheltema 1976, 1989) (Fig. 4C, F).

The family is comprised of three genera, *Chaetoderma*, *Caudosfoveatus*, and *Falcidens*. *Falcidens* is represented by 202 specimens and two species, *F. chiastos* and *F. lipuros*, in recent collections from the Australian shelf. Generic identification of another single specimen is undetermined.

Body regions vary in relative length among species. Within a species body regions may bear morphologically similar or dissimilar spicules. Spicules can be rather plain or ornamented with numerous ridges as in *Falcidens chiastos* and there is often a medial keel. The denticles of the radula in *Chaetoderma* are connected to the cone by thin lateral projections and are separate from each other, whereas in *Falcidens* the denticles are pincers-like and arise from a common base attached to the cone (Salvini-Plawen 1968a; Scheltema 1972). Bolsters are not chondroid but are formed of anastomosed muscle fibers and connective tissue. They lie between

the cone and cuticular membranes that rest on the outside of the buccal mass. Remains in the gut show that chaetodermatids are selective carnivores on foraminifera, small snails, worms, and perhaps crustaceans and other organisms. It is not known whether there is food specificity within a species. The pericardium often has large lateral extensions. In some species there is an aortal bulb and a ventricle which is capable of great expansion (Scheltema 1973). Auricles are generally paired.

*Falcidens chiastos* was collected from fine muds, fine sands and shell in Bass Strait between 22 and 120 m at densities up to 180 m<sup>-2</sup>. The species is closely related to *F. loveni* from the Java Sea and to an undescribed species from the slope east of Bass Strait, as well as to two species from the western Atlantic shelf and slope. A second species from Bass Strait, *F. lipuros*, occurs at depths greater than 100 m and continues down onto the slope. It also shows affinities to an East Indies species, *F. wireni*. The genus *Chaetoderma*, common on continental shelves worldwide, has not been collected on the Australian shelf, although there is a slope species, *C. usitatum*, that occurs at depths greater than 1,000 m (Scheltema 1989).

#### Prochaetodermatidae

Members of the Prochaetodermatidae are small, less than 6 mm long, and are recognized by a divided oral shield, a tail-like posterium, and by large, paired pharyngeal cuticular jaws (Scheltema, 1985, 1989) (Fig. 5).

The family is known from two genera, *Prochaetoderma* and *Rhabdoderma*, at slope depths (Scheltema 1989 and unpublished data). A single specimen from the shelf lacks its spicules, upon which generic determinations are made, but, from size and shape, is a different species from those on the slope. These records from the Australian slope and shelf are the first in the west Pacific for any species in this family, which is now known to be distributed worldwide from shelf to hadal depths over 7,000 m.

#### Subclass Neomeniomorpha

The neomenioids are creepers, recognized by the presence of a ventral furrow, or groove, often visible only as a thin line, within which lies a narrow foot, and by the absence of an oral shield. A few species in the Neomeniidae and Epimeniidae are the largest known aplacophorans. There are 23 named families with 71 genera and 194 species worldwide.

The number of neomenioid species collected from the Australian continental shelf and Macquarie Island has been expanded from 2 reported previously to 29 reported here, and from 2 to 14 or 15 genera in 9 or 10 families. However, the descriptions of only eight families are included below because generic and familial relationships of single specimens belonging to two species have not been determined.

The integument and spicules together form a character that link genera or families to one another (Salvini-Plawen 1978b). A thin cuticle usually bears thin, flat spicules as in the Dondersiidae or Lepidomeniidae (Figs. 6, 7). Short, solid spicules are nearly upright in the thick cuticle of the Neomeniidae. A number of genera have a thick cuticle with either solid or hollow elongate spicules that are parallel to the body and cross over each other at 90°. They are arranged so that they run from ventro-anterior to dorso-posterior and from dorso-anterior to ventro-posterior, thus forming a strong, reticulated, skeletal network (Figs. 10, 11). These

spicules are here called *skeletal* (also called *tangential*). There may be spicules in a variety of shapes, e.g., paddles, hooks, or scoops, which extend beyond the cuticle and are here called upright spicules (called *radial* in other works). The morphology of upright spicules in conjunction with radula type is used here to define families.

Neomenioid species creep by means of their protruded, ciliated foot along a sticky mucous track produced from the ciliated, eversible pedal pit at the anterior end of the pedal groove (Fig. 1B). Movement is reported to be entirely by ciliary action (Pruvot 1891; Salvini-Plawen 1968b). The pedal pit is supplied by many mucous glands which continue along the entire foot groove and empty into it. Some species have been observed to spin a mucous thread when dislodged from the wall of the vessel in which they were being observed (Pruvot 1891). In *Epimenia*, the pedal pit is used as a sucker (Baba 1940b). Anterior to the pedal pit the head end is held above the substratum and freely moved. *Neomenia* has been described as burrowing by means of its proboscis-like pharynx (Wirén 1892b).

Neomeniomorpha are known from gut contents or attachment to their prey to feed on cnidarians -- hydrozoans, zooantharians, gorgonians, or stony corals. There is sometimes a host specificity. Other food sources are conjectural (Salvini-Plawen 1981). The mouth may open in common with the sensory vestibule which lies above it, or mouth and vestibule may open separately (Fig. 1B). Circular muscles surround the pharynx, sometimes in series of bands, whose presence suggests the function of a buccal pump. The pharynx is sometimes protrusible and proboscis-like. The radula may be large to very small or even absent. It is rather far back from the mouth and lies where the pharynx joins the midgut unless an esophagus is present. In some families the distal rows of teeth bend ventrally into paired or single anteroventral pockets (Fig. 1B). Digestion starts in the pharynx (Baba, 1940b) which is well supplied by secretory glands. There is nearly always a pair of discrete ventral salivary glands that open into the pharynx at the level of the radula. In addition there are diffuse, separate gland cells or distinct, paired or single dorsal glands. The ventral salivary glands include different morphological types, which have been used to classify families (Salvini-Plawen 1978b).

The midgut serves both as stomach and digestive gland. In the Epimeniidae experimentation has shown that cells lining the cavity are the site for extracellular and intracellular digestion. There is often a single or paired anterior extension of the midgut, called a dorsal coecum, above the pharynx. The lumen of the midgut in histologic preparations is filled with unexploded nematocysts. A dorsal ciliated typhlosole runs the length of the midgut, which passes posteriorly into the ciliated hindgut, or intestine. The latter bends ventrally and opens into the mantle cavity.

All neomenioids are hermaphroditic and have paired gonads. Ova usually are produced on the medial walls and spermatozoa on the lateral walls. The reproductive system has many elaborations but follows the general plan of paired U-shaped gametoducts passing from pericardium to the mantle cavity. A vastly expanded pericardium serves as a sort of specialized sac in *Eleutheromenia* (Pararrhopalidae). In *Phyllomenia* true gonaducts pass from the gonads directly to mantle cavity pockets (Salvini-Plawen 1970). There are usually one to many seminal receptacles, which sometimes are stalked, where the upper and lower gametoducts join (Fig. 1B). There may be seminal vesicles along the upper gametoduct near the pericardium. The lower gametoducts are large and lined along their length with secretory cells and function as shell glands (Baba 1940b). The lower gametoducts may open on paired gametopores, or they may

unite for most of their length or only terminally and open on a single gametopore which is sometimes a muscular penial sheath. Paired, protrusible copulatory spicules are present in many families (Figs. 7, 9, 11). They range in structure from a pair of single, simple or helical needles to paired groups of two or more and are sometimes 1/3 or more total body length. Their morphology is sometimes elaborate. There are often specialized spicules on each side of the inner mantle cavity wall which appear to be accessory to the copulatory spicules. Copulatory spicules have seldom been used to characterize or discriminate among species, but their potential taxonomic importance is shown by two species of *Eleutheromenia* (Pararrhopalidae) in Bass Strait which are nearly indistinguishable except for slight, nonoverlapping differences in the morphology of their copulatory spicules.

The most important taxonomic characters that are used in the identification and classification of the Neomeniomorpha in addition to those used in the Chaetodermomorpha are morphology of the copulatory spicules if present, height and breadth of the anterior and posterior body, spicule arrangement along the foot groove, shape of integumental papillae, type of ventral salivary glands, and elaborations of the reproductive system.

For most neomenioids, especially the numerous small species, the radula and copulatory spicules are not easily dissected. In such cases, the entire anterior and posterior ends may be cut away from the midbody and the tissue removed with hypochlorite or KOH. Internal anatomy is ascertained from histologic sections, for which trichrome stains give excellent differentiation amongst various glands. If integumental spicules are not easily dislodged by teasing, a portion of the intact integument can be placed in hypochlorite to remove the cuticle. Other techniques are as described for the Chaetodermomorpha.

#### Key to the families of Australian continental shelf Neomeniomorpha

1. (a) Spicules birefringent, dissolve in acid . . . . . 2  
     (b) Spicules not birefringent, do not dissolve in acid. . . . . Notomeniidae
2. (a) Skeletal (tangential) spicules absent . . . . . 3  
     (b) Skeletal (tangential) spicules present . . . . . 6
3. (a) Spicules solid, extend upright from cuticle . . . . . 4  
     (b) Spicules solid, flat-lying, scale-like . . . . . 5
4. (a) Many harpoon-shaped spicules . . . . . Neomeniidae  
     (b) Few fishhook-shaped spicules . . . . . Pararrhopalidae
5. (a) Spicules of two types, animal >5 mm, dorsally carinate . . . . Dondersiidae  
     (b) Spicules of one type, animal <3 mm, no dorsal  
         carina, copulatory spicules evident . . . . . Lepidomeniidae
6. (a) Animal 20 mm or more long and slender . . . . . 7  
     (b) Animal <20 mm long, slender or broad . . . . . 8
7. (a) Radula with 2 teeth per row, >80 mm long . . . . . Epimeniidae  
     (b) Radula with many teeth per row, <80 mm long . . . . . Proneomeniidae
8. (a) Upright spicules paddle-shaped. . . . . Phyllomeniidae  
     (b) Upright spicules fishhook-shaped . . . . . Pararrhopalidae

### Family Dondersiidae

Members of the family Dondersiidae have a unique, tiny monostichous radula (one tooth per row) in which the two medial denticles are fused at their distal tips. The radula is sometimes lacking. Two types of spicules are present. One is paddle-shaped and the other is somewhat oval and may or may not have a proximally thickened rim. The posterior end of the body is usually drawn out to a point and covers the mantle cavity opening (Salvini-Plawen 1978b).

A single specimen of a new species of *Nematomenia* recently was taken in Bass Strait with a rock dredge. The specimen was probably dislodged from a hydrozoan upon which members of this genus are known to feed (Pruvot 1891; Heath 1911).

Species are slender and even within a genus may vary from only a millimeter or two to 40 mm. A dorsal carina is often present. Discrete dorsal lobate salivary glands may be present or absent and are not a distinctive generic character. The paired ventral salivary glands are often small. Gill folds are often absent. In some genera mantle cavity pockets are present. A dorsoterminal sensory organ may or may not be present. Both seminal vesicles and seminal receptacles are usually present, though copulatory spicules are usually lacking. There is a single gametopore.

The family is very widely distributed in the world oceans, including the eastern and western Pacific, the Arctic and Antarctic, the northeastern and northwestern Atlantic, and the Mediterranean. Certain species of *Nematomenia* appear to be very widespread. *N. platypoda* occurs in the Aleutians and (unpublished) in the Gulf of California, and *N. flavens* has been taken from off the Shetlands and in the Mediterranean. Thus the single specimen from Australia could belong to a wide-ranging species.

### Lepidomeniidae

The family Lepidomeniidae is comprised of species that have overlapping, leaf-like spicules whose form is uniform within a species and that possess a radula with distichous rows of teeth in the form of denticulated hooks. They differ from the very similar Gymnomeniidae Odhner 1921 (= Wireniidae Salvini-Plawen 1978b) in the form of the ventral salivary glands and the lack of statocysts (Salvini-Plawen 1988a). A species of *Tegulaherpia*, *T. tasmanica*, has been reported from Bass Strait (Salvini-Plawen 1988a).

The species are small, usually less than 3.5 mm in length, translucent, and glistening with a silky sheen. The leaf-like spicules are thin, 4  $\mu$ m or less. Most species have paired copulatory spicules with 2 or more spicules per pair. Integumental unstalked papillae are present in the thin cuticle. The pedal pit is usually large and protrusible. Paired ventral salivary glands are follicular and possess a duct. The dorsal salivary glands are diffuse. Midgut sacculations are usually only weakly formed or are absent. There is a single gametopore, which often opens on a large, muscular, penial papilla.

Lepidomeniid species are meiofaunal forms found in sands and sandy muds. In Bass Strait, five new species of *Tegulaherpia* have been collected from 55 to 140 m depth and another new species occurs in Cleveland Bay off Townsville, Queensland. The family has previously been reported only from the eastern, western, and southern Atlantic Ocean and Mediterranean Sea.

#### Family Notomeniidae (unpublished family name)

The monogeneric family Notomeniidae is unique in that its members possess noncalcareous spicules. It is monotypically represented by *Notomenia clavigera* Thiele 1897, which was described from a single specimen taken at 37 m in Torres Strait. The unusual occurrence of haemotoxylin-staining spicules (Thiele 1902c) was corroborated by a second specimen recently collected in Bass Strait from 40 m. Spicules show no birefringence under cross-polarized light, nor do they dissolve in hydrochloric acid.

*Notomenia clavigera* is 4 mm or less in length, brown, and bears club-shaped spicules up to 100 µm long and 15 µm wide. The mouth is surrounded by a rim. The mantle cavity is overlain by a knob-like protuberance. Radula, copulatory spicules, gill-folds, and dorsoterminal sensory organ are lacking. Unique are (a) the ring of ganglia surrounding the vestibule; (b) the position of the mantle cavity dorsal to the pericardium, gametoducts, and intestine; (c) the opening of paired gametopores directly to the outside and not into the mantle cavity; (d) the dorsal opening of the intestine into the mantle cavity; and (e) the openings of the pericardium into the upper gametoducts anterior to the bend between upper and lower gametoducts.

The affinities of this unique species and family are not known.

#### Family Neomeniidae

Species in the monogeneric family Neomeniidae may be very large, measuring more than 100 mm in length, and breadth is one-third the length. The spicules form a shiny fuzz on the distinctive, plump body rounded at both ends. The cuticle is thick, with large epidermal papillae and a distinctive combination of trowel-shaped, harpoon-like, and solid needle-shaped spicules (Salvini-Plawen 1978b). Harpoon-like spicules are held in common with the Hemimeniidae Salvini-Plawen 1978, which differ from the Neomeniidae by having a thin cuticle, no papillae, and a polystichous radula (many teeth per row).

Five specimens of a new *Neomenia* species, the largest nearly 6 mm long by 2.5 mm in diameter, have been collected in Bass Strait at 140 m.

The body in several species has a dorsal carina. There is a thick, dense dermis lying directly beneath the epidermis. It consists of a homogeneous matrix in which are embedded muscle fibers, nerve fibers, and blood spaces containing blood cells. There is no radula. The pharynx is ringed by heavy muscles and can be everted. Salivary glands are lacking. The midgut is sacculate. Gill folds are present. There are vestibular papillae and a dorsoterminal sensory organ. Copulatory spicules coupled with accessory glands are present and there is a single gametopore.

Neomeniidae have been collected from the eastern and western north Atlantic, the Mediterranean, the sub-Arctic and sub-Antarctic, and from northern Japan. The largest species occur at latitudes of 42° or greater.

#### Family Phyllomeniidae

Members of the Phyllomeniidae have solid skeletal spicules and upright paddle-shaped spicules, a distichous radula with denticulated hook-like teeth, and usually a pointed posterior covering the mantle cavity. The family definition (Salvini-Plawen 1978b) is here provisionally expanded to include species with hollow skeletal spicules.

Eleven specimens in two genera and three species of Bass Strait neomenioids provisionally are placed in this family. At least one of the genera is new and has a unique radula (Fig. 10D).

Species of Phyllomeniidae are slender and 12 mm or less in length. The upright paddle-shaped spicules are conspicuous, sometimes producing a glitter against a smooth background. The thick cuticle bears plump papillae. Gill folds are lacking. A dorsoterminal sensory organ is usually present. The reproductive system in *Phyllomenia* is unique in having true gonaducts. Gonopericardial ducts are absent in adults and the gonads empty directly into mantle cavity pockets. Copulatory spicules and usually seminal vesicles and seminal receptacles are present.

The Phyllomeniidae have previously been collected only from the Antarctic and sub-Antarctic south of 52°S. The Bass Strait species extends the family's range to north of 40°S.

#### Family Pararrhopalidae

The presence of fishhook-like upright spicules, either solid or hollow, here defines the family Pararrhopalidae, members of which may be spiny or smooth and range as adults from 2 to 12 mm in length. All genera have skeletal integumental spicules except *Ocheyoherpia*, which has upright spicules only, although in *O. lituifera* the upright spicules cross each other. *Ocheyoherpia* is provisionally removed from the Phyllomeniidae, a redefinition of the family (Salvini-Plawen 1978b).

Species of Pararrhopalidae are the most numerous and diverse neomenioids in Australia. There is great radiation within some genera, within which morphologically very similar species occur. Including Macquarie Island, there are 13 species in 6 genera. Among the total 172 specimens of Neomeniomorpha collected in Bass Strait, 110 or nearly two-thirds belong to 11 pararrhopalid species. Pararrhopalidae occur at two-thirds of the localities in Bass Strait where Aplacophora were collected and one species of *Eleutheromenia* accounts for nearly one-third of all neomeniomorph specimens.

The Pararrhopalidae forms a morphologically diverse group. The fishhook-like spicules may be so abundant that they are easily observed in situ through a dissecting microscope (Fig. 11A), or they may be so sparse that they could be overlooked without resorting to examination of a specimen at magnification of 160X or more under a compound light microscope (Fig. 11E). Some species are short and stubby, less than 4.5 mm, and very spiny or somewhat rough, whereas others may be thin and up to 8 mm, and either spiny or smooth. Integumental papillae may be present or absent; if present, they may be club-shaped. The radula is distichous with denticulated hook teeth. In *Ocheyoherpia* the outside tooth is doubled in an inverted V shape. Paired dorsal salivary glands that open through a papilla into a dorsal pharyngeal pocket may be present or absent. Copulatory spicules with or without accessory glands may be present or absent. In *Eleutheromenia*, there is a large accessory "ovigerous" gland connected with the pericardium. Gill folds may be present as papillae or as only a few low folds.

In addition to the numerous new species found in Bass Strait, a new species of *Pararrhopalia* has been collected in Halifax Bay, north Queensland, and several specimens of a species of *Ocheyoherpia* were collected by divers at Macquarie Island from shallow depths (6-14 m). Two new pararrhopalid species from the deepest locality at 140 m in Bass Strait also occur in a sample from the adjacent continental slope at 400 m, where there is the same diversity and high numbers of Pararrhopalidae as in the continental shelf stations of Bass Strait (Scheltema 1990).

The genera *Eleutheromenia* and *Pararrhopalia* were first reported from the Mediterranean (Pruvot 1891) and *Ocheyoherpia* from the sub-Antarctic Atlantic Ocean (Salvini-Plawen 1978b). Six new species of an elongate, smooth Pararrhopalidae belong to a new, yet unnamed genus that so far is known only from Australia (Fig. 11E).

#### Family Proneomeniidae

The family Proneomeniidae is defined by a polystichous radula (many teeth per row) and an elongate, smooth body with hollow skeletal spicules and small upright paddle-shaped spicules. There are two genera, *Proneomenia* and *Dorymenia*.

A single specimen of *Dorymenia*, *D. harpagata*, has been described from 100 m off Macquarie Island (Salvini-Plawen 1978b).

The family includes some of the largest of the elongate neomenioids, ranging up to 130 mm in length in the Arctic. *D. harpagata* is one of the small species, 20 mm in length. The posterior end of *Dorymenia* species is sometimes produced into a finger-like projection. Species may be tricarinate (with three longitudinal body ridges) as in *D. harpagata*, or quincarinate. The small upright spicules are scarcely evident above the smooth body with many layers of skeletal spicules within a thick cuticle. Epidermal papillae are numerous and have long, sometimes branched stalks. The ventral salivary glands are tubular and very long, extending posteriorly beneath the midgut. There are deep mantle cavity pockets, numerous accessory copulatory spicules in the mantle cavity wall, and a single gametopore. The presence of a pair of single copulatory spicules distinguishes *Dorymenia* from *Proneomenia*, where they are lacking, but they appear to be resorbed in *Dorymenia* (personal observation). *D. harpagata* has up to five dorsoterminal sensory organs.

The family is speciose and widespread, found from the Arctic to the Antarctic and in both the eastern and western Atlantic and Pacific Oceans from the shelf to 3,000 m. It was not collected from Bass Strait.

#### Family Epimeniidae

Species in the monogeneric family Epimeniidae are elongate and among the largest Aplacophora, some specimens measuring up to 30 cm in length by 1 cm in diameter. In life they are colorful, orange-red to dark brown, with a chrome-yellow dorsal stripe or with bright violet, yellow, green or blue prominences (Nierstrasz 1902; Baba 1939, 1940a). Skeletal and upright spicules are hollow and needle-shaped. The anterior end of the body is rounded, the posterior tapered. The radula is distichous, with denticulated hook-like teeth.

The first species of *Epimenia* was described from a single specimen collected at 108 m off northwestern Australia, *E. australis* (Thiele 1897). Eleven more specimens taken nearby between 32 and 112 m by the Siboga Expedition were described as *E. verrucosa*. Until new specimens are collected it will not be known whether the two species are synonyms (cf. Nierstrasz 1902 and Thiele 1902c). A third species, *E. oshimai*, has been described from southern Japan (Baba 1940a).

Its size and ease with which it is collected off Amakusa, Japan, made *E. verrucosa* a unique source for observation and experimentation (Baba 1940b). There are two or three types of integumental papillae with small, bulbous ends on long, narrow stalks. The contents of the papillae give the body color. The pedal gland excretes mucus exclusively. The pedal pit, or



cavity, produces a fine thread of mucus along which the animal glides snail-like on its long, narrow foot. The inner portion of the pedal cavity can be everted hydrostatically, and the pit can then act as a sucker. In Japan, *E. verrucosa* feeds on the coenosarc and polyps of two species of alcyonarians. The foregut can be everted like a proboscis, bringing the radula to the exterior, but feeding was not observed. The ventral salivary glands are long and tubular, with a glandular section and a long duct. Extracellular digestion starts in the pharynx. In the midgut both extracellular and intracellular digestion take place, the latter preceded by phagocytosis of particles by the club-shaped cells of the villi which line the midgut. At senescence, the villous cells contain vacuoles with uric acid crystals and are released into the lumen of the midgut. Nematocysts are seldom taken up by the villous cells but remain in the lumen. Shed cells and undigested material are passed to the intestine and into the mantle cavity.

Erythrocytes (most numerous), amoebocytes, and platelets are distributed in the heart, sinuses, and haemocoel around the digestive tract, and especially in lacunae at the tips of the midgut villi. Injected black ink is phagocytized by the amoebocytes, which discharge the ink particles directly into the midgut lumen between the villous cells. They do not discharge into the integumental papillae.

There are no copulatory spicules. The pericardium is large. Seminal vesicles are numerous and stalked. The lower gametoducts unite and empty through a single gametopore. Individuals of *E. verrucosa* are mature at 9 cm. In Japan the breeding season is from June to October (Baba 1951). In *E. verrucosa* spawn is laid as a pair of flat mucous bands each bearing 40 or more either uncleaved eggs or developing larvae after a period of brooding. Development from egg to larva, whether spawned or brooded, requires about 4 days, and the larvae swim for only two days after release before settling and metamorphosis. Developmental studies of Baba (1938, 1940c, 1951) provide the only evidence for spiral cleavage in the Aplacophora.

The Epimeniidae appears to be a widespread family in tropical West Pacific waters at 100 m or less. Divers recently have collected *E. verrucosa* at 10 m in Tolo Harbor, Hong Kong, and two unidentified species between 15 and 33 m in New Caledonia (author's unpublished data). Although *Epimenia* has only once been collected from the Australian shelf, it can be expected among corals, particularly alcyonarians, or on coral sands of tropical Australia.

## Literature Cited

- Baba, K. (1938). The later development of a solenogastre, *Epimenia verrucosa* (Nierstrasz). *Journal of the Department of Agriculture, Kyusyu Imperial University* 6: 21-40
- Baba, K. (1939). Preliminary note on *Epimenia verrucosa* (Nierstrasz), a solenogastre species from Amakusa, Japan. *Venus (Tokyo)* 9: 35-42
- Baba, K. (1940a). *Epimenia ohshimai* a new solenogastre species from Amakusa, Japan. *Venus (Tokyo)* 10: 91-96
- Baba, K. (1940b). The mechanisms of absorption and excretion in a solenogastre, *Epimenia verrucosa* (Nierstrasz), studied by means of injection methods. *Journal of the Department of Agriculture, Kyusyu Imperial University* 6: 119-166
- Baba, K. (1940c). The early development of a solenogastre, *Epimenia verrucosa* (Nierstr.). *Annotationes Zoologicae Japonenses* 19: 107-113
- Baba, K. (1951). General sketch of the development in a solenogastre, *Epimenia verrucosa* (Nierstrasz). *Miscellaneous Reports of the Research Institute for Natural Resources (Japan)* 19-21: 38-46
- Beedham, G.E. & E.R. Trueman (1968). The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. *Journal of Zoology* 154: 443-451
- Boss, K.J. (1982). Mollusca. pp. 945-1166 in Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. Vol. 1. New York: McGraw Hill
- Buckland-Nicks, J. & F.-S. Chia (1989). Spermiogenesis in *Chaetoderma* sp. (Aplacophora). *Journal of Experimental Zoology* 252: 308-317
- Deimel, K. (1982). Zur Ableitung des Radulaapparates der Chaetodermatidae (Mollusca, Caudofoveata). *Zeitschrift für zoologisches Systematik und Evolutionsforschung* 20: 177-187.
- Gage, J.D. (1991). *Deep-sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge: Cambridge University Press.
- Franzén, Å. (1955). On the spermiogenesis in Solenogastres. *Zoologiska Bidrag från Uppsala* 30: 485-491.
- Haas, W. (1981). Evolution of calcareous hardparts in primitive molluscs. *Malacologia* 21: 403-418

Hadfield, M.G. (1979). Aplacophora. pp. 1-25 in Giese, A.C. & Pearse, J.S. (eds.) *Reproduction of Marine Invertebrates Vol. 5. Molluscs: Pelecypods and Lower Classes*. New York : Academic Press

Haszprunar, G. (1986). Feinmorphologische Untersuchungen an Sinnesstrukturen ursprüngliche Solenogastres (Mollusca). *Zoologischer Anzeiger* 217: 345-362

Haszprunar, G. (1987). The fine morphology of the osphradial organs of the mollusca. IV Caudofoveata and Solenogastres. *Philosophical Transactions of the Royal Society of London B*, 315: 63-73

Heath, H. (1904). The nervous system and subradular organ in two genera of solenogastres. *Zoologische Jahrbücher (Abteilung für Anatomie und Ontogenie der Tiere)* 20: 399-408

Heath, H. (1911). The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific...by the "Albatross". *Memoirs of the Museum of Comparative Zoology (Harvard University)* 45: 1-179

Heath, H. (1912). *Spengelomenia*, a new genus of solenogastres. *Zoologische Jahrbücher, Supplement* 15: 465-478

Heath, H. (1918). Solenogastres from the Eastern Coast of North America. *Memoirs of the Museum of Comparative Zoology (Harvard University)* 45: 185-263

Hoffman, S. (1949). Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. *Zoologiska Bidrag från Uppsala* 27: 293-427

Hyman, L.H. (1967). *The Invertebrates. Vol. VI. Mollusca I*. New York : McGraw-Hill  
vii + 792 pp.

Ivanov, D.L. (1979). Structure and functional morphology of radular system in *Chaetoderma* (Mollusca, Caudofoveata). *Zoologicheskii Zhurnal* 58: 1302-1306

Ivanov, D.L. (1984). Caudofoveats (Mollusca, Caudofoveata) in Peter the Great Bay. pp. 28-41 in A.I. Kafanov (ed.), *Hydrobiological research of bays and inlets of Primorye*. Far East Science Center, USSR Acad. Sci. Vladivostok

Morse, M.P. (1979). *Meiomenia swedmarki* gen. et. sp. n., a new interstitial solenogaster from Washington, USA. *Zoologica Scripta* 8: 249-253

Morse, M.P. and Scheltema, A.H. (1988). Aplacophora. pp. 447-450 in Higgins, R.P. and Thiel, H. (eds.) *Introduction to the Study of Meiofauna*. Washington, D.C. and London: Smithsonian Institution Press

- Nierstrasz, H.F. (1902). The solenogastres of the Siboga-Expedition. *Siboga-Expeditie* 47: 1-46
- Ponder, W.F. (1970). A new aplacophoran from New Zealand. *Journal of the Malacological Society of Australia* 2: 47-54
- Pruvot, G. (1890). Sur le développement d'un Solénogastre. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences* 111: 689-692
- Pruvot, G. (1891). Sur l'organisation de quelques néoméniens des côtes de France. *Archives de Zoologie expérimental et général, series 2*, 9: 699-806
- Pruvot, G. (1892). Sur l'embryogénie d'une *Proneomenia*. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences* 114: 1211-1214
- Salvini-Plawen, L.v. (1967). Neue scandinavische Aplacophora (Mollusca, Aculifera). *Sarsia* 27: 1-63
- Salvini-Plawen, L.v. (1968a). Über Lebendbeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia* 31: 105-126
- Salvini-Plawen, L.v. (1968b). Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Sarsia* 31: 131-142
- Salvini-Plawen, L.v. (1969). Faunistische Studien am Roten Meer im Winter 1961/62 : V. Caudofoveata und Solenogastres (Mollusca, Aculifera). *Zoologische Jahrbucher (Abteilung für Systematik, Ökologie und Geographie der Tiere)* 96: 52-68
- Salvini-Plawen, L.v. (1970). *Phyllomenia austrina*, ein phylogenetisch bedeutsamer Solenogaster (Mollusca, Aculifera). *Zeitschrift für zoologisches Systematik und Evolutionsforschung* 8: 297-309
- Salvini-Plawen, L.v. (1972). Zur Morphologie und Phylogenie der Mollusken : Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Zeitschrift für wissenschaftliche Zoologie* 184: 205-394
- Salvini-Plawen, L.v. (1978a). Different blood-cells in species-pairs of Solenogastres (Mollusca). *Zoologischer Anzeiger* 200: 27-30
- Salvini-Plawen, L.v. (1978b). Antarktische und subantarktische Solenogastres (eine Monographie: 1898-1974). *Zoologica (Stuttgart)* 44: 1-315
- Salvini-Plawen, L.v. (1981). The molluscan digestive system in evolution. *Malacologia* 21: 371-401
- Salvini-Plawen, L.v. (1985a). New interstitial solenogastres (Mollusca). *Stygologia* 1: 101-108

- Salvini-Plawen, L.v. (1985b). Early evolution and the primitive groups. pp. 59-160 in Trueman, E.R. & Clarke, M.R. (eds.) *The Mollusca*, Vol. 10, *Evolution*. Orlando : Academic Press, Inc.
- Salvini-Plawen, L.v. (1988a). Einige Solenogastres (Mollusca) der europäischen Meiofauna. *Annalen des naturhistorischen Museums in Wien* 90(B): 373-385
- Salvini-Plawen, L.v. (1988b). The structure and function of molluscan digestive systems. pp. 301-379 in Trueman, E.R. & Clarke, M.R. (eds.) *The Mollusca*. Vol. 11. *Form and function*. San Diego and other cities : Academic Press, Inc.
- Sanders, H.L., Hessler, R.R., & Hampson, G.R. (1965). An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep-Sea Research* 12: 845-867
- Scheltema, A.H. (1972). The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere* 72: 361-370
- Scheltema, A.H. (1973). Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere* 76: 97-107
- Scheltema, A.H. (1976). Two new species of *Chaetoderma* from off west Africa (Aplacophora, Chaetodermatidae). *Journal of Molluscan Studies* 42: 223-234
- Scheltema, A.H. (1978). Position of the class Aplacophora in the phylum Mollusca. *Malacologia* 17: 99-109
- Scheltema, A.H. (1981). Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia* 20: 361-383
- Scheltema, A.H. (1985). The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca : Chaetodermomorpha). *Biological Bulletin (Woods Hole)* 169: 484-529
- Scheltema, A.H. (1987). Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongrei*. *Marine Ecology-Progress Series* 37: 171-180
- Scheltema, A.H. (1988). Ancestors and descendents : relationships of the Aplacophora and Polyplacophora. *American Malacological Bulletin* 6: 57-68
- Scheltema, A.H. (1989). Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off southeastern Australia. *Records of the Australian Museum* 41: 43-62

- Scheltema, A.H. (1990). The Aplacophora as a Tethyan slope taxon: evidence from the Pacific. *Bulletin of Marine Science* 47: 50-61
- Scheltema, A.H., Buckland-Nicks, J., & Chia, F.-S. (1991). *Chaetoderma argenseum* Heath, a northeastern Pacific aplacophoran mollusk redescribed (Chaetodermomorpha: Chaetodermatidae). *Veliger* 34: 204-213
- Scheltema, A.H. & Kuzirian, A.M. (1991). *Helicoradomenia juani*, gen. et. sp. nov., a Pacific hydrothermal vent Aplacophora (Mollusca: Neomeniomorpha). *Veliger* 34: 195-203
- Scheltema, A.H., Tscherkassky, M., & Kuzirian, A.M. (In press). Aplacophora. In Harrison, F.W. & Kohn, A.J. (eds.) *Microscopic Anatomy of Invertebrates*. Vol. 5: *Mollusca: Monoplacophora, Aplacophora, Polyplacophora, and Gastropoda*. New York: Wiley-Liss
- Scheltema, A.H., M. Tscherkassky, & A.M. Kuzirian (In press). Aplacophora in Harrison, F.W. (3d.) *Microscopic Anatomy of Invertebrates* Vol. V *Mollusca* 1. New York: Wiley-Liss
- Schwabl, M. (1955). *Rupertomenia fodiens* nov. gen. nov. sp. eine neue Lepidomeniide von der Sudwestküste Schwedens. *Osterreichische zoologische Zeitschrift* 6: 90-146
- Selenka, E. (1885). Report on the *Gephyrea* collected by H.M.S. Challenger during the years 1873-1876. *Report on the Scientific Results...of H.M.S. Challenger* 13(2): 25 pp.
- Stork, H.A. (1941). Solenogastren der Siboga-Expedition. *Siboga-Expeditie* 47b: 45-70
- Thiele, J. (1897). Zwei australische Solenogastres. *Zoologischer Anzeiger* 20: 398-400
- Thiele, J. (1902a). *Proneomenia amboinensis* n.sp. *Denkschriften der Medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 8: 733-738
- Thiele, J. (1902b). *Proneomenia valdiviae* n.sp. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition Valdivia 1898-1899* 3: 167-174
- Thiele, J. (1902c). Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie* 72: 249-466
- Thiele, J. (1906). *Archaeomenia prisca* n.g., n.sp. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition Valdivia 1898-1899* 9: 315-324
- Thompson, T.E. (1960). The development of *Neomenia carinata* Tullberg (Mollusca Aplacophora). *Proceedings of the Royal Society of London B* 153: 263-278

Wirén, A. (1892a). Studien über die Solenogastren. I. Monographie des *Chaetoderma nitidulum* Lovén. *Svenska Vetenskapsakademiens Handlingar* 24(12): 1-66

Wirén, A. (1892b). Studien über die Solenogastren. II. *Chaetoderma productum*, *Neomenia*, *Proneomenia acuminata*. *Svenska Vetenskapsakademiens Handlingar* 25(6): 1-100.

### Captions

Figure 1. Semischematic sagittal sections of aplacophorans. a, *Limifossor talpoideus* of the subclass Chaetodermomorpha; b, *Spengelomenia bathybia* of the subclass Neomeniomorpha (a, after Heath 1911; b, after Heath 1912.)

Figure 2. The nervous system of *Micromenia fodiens* of the subclass Neomeniomorpha. (After Schwabl 1955.)

Figure 3. Development of *Neomenia*. a-b, 4- and 3-day larvae, respectively; c-d, 10-day larvae. (After Thompson 1960.)

Figure 4. Australian Chaetodermatidae from Bass Strait. a-d, *Falcidens chiastos*; e-g, *Falcidens lipuros*; b, oral shield, which is entire; c & f, radula; d & g, spicules. (From Scheltema 1989.)

Figure 5. Australian Prochaetodermatidae. *Rhabdoderma australe* from a depth of 1,200 m off New South Wales; a, ventral view showing divided oral shield; b, whole animal; c, radular tooth; d, jaw. (From Scheltema 1989.)

Figure 6. Australian Dondersiidae. Genus *Nematomenia* from Bass Strait. a, whole animal; b, spicules. Radula probably lacking.

Figure 7. Australian Lepidomeniidae. Genus *Tegulaherpia* from Bass Strait. a, whole animal; b, spicule, proximal (lower) end thickened; c, distal half of copulatory spicules; d, single tooth from right side of radula.

Figure 8. Australian Notomeniidae. *Notomenia clavigera* from Bass Strait. a, whole animal, most of the spicules have been lost from specimen; b, club-shaped and rimmed non-calcareous spicules.

Figure 9. Australian Neomeniidae. Genus *Neomenia* from Bass Strait. a, whole animal; b, harpoon-like spicule; c, trowel-shaped spicule; d, needle-shaped spicule; e, distal part of copulatory spicules with thickened ends, distal-most ends missing.

Figure 10. Australian ?Phyllomeniidae. a-c, genus ?*Phyllomenia* from Bass Strait; d-g, new genus from Bass Strait; b, f, h, upright spicules; c, g, skeletal spicules; e, single tooth from left side of radula.

Figure 11. Australian Pararrhopalidae. a-e, genus *Eleutheromenia* from Bass Strait; f-h, new genus from Bass Strait. b, c, h, upright spicules; g, hollow skeletal spicule; e, single radular row of teeth, denticle number of teeth unequal.



Figure 12. Proneomeniidae. *Dorymenia*, eastern Atlantic and Macquarie Island. a, whole animal, new Atlantic species; b, copulatory spicule of same; c-f, *D. sarsii*, Norway; c, one row of radular teeth; d, accessory copulatory spicule from mantle cavity wall; e, upright, solid paddle-shaped spicule; f, hollow skeletal spicule; g, lateral and medial pair of radular teeth, *D. harpagata*, Macquarie Island (after Salvini-Plawen 1978b).

Figure 13. Pacific Epimeniidae. *Epimenia verrucosa* (= *E. ?australis*) from Amakusa, Japan. a, whole animal; b, hollow spicule; c, portion of radula, teeth of same and adjoining rows with unequal denticles. (From Baba 1939.)



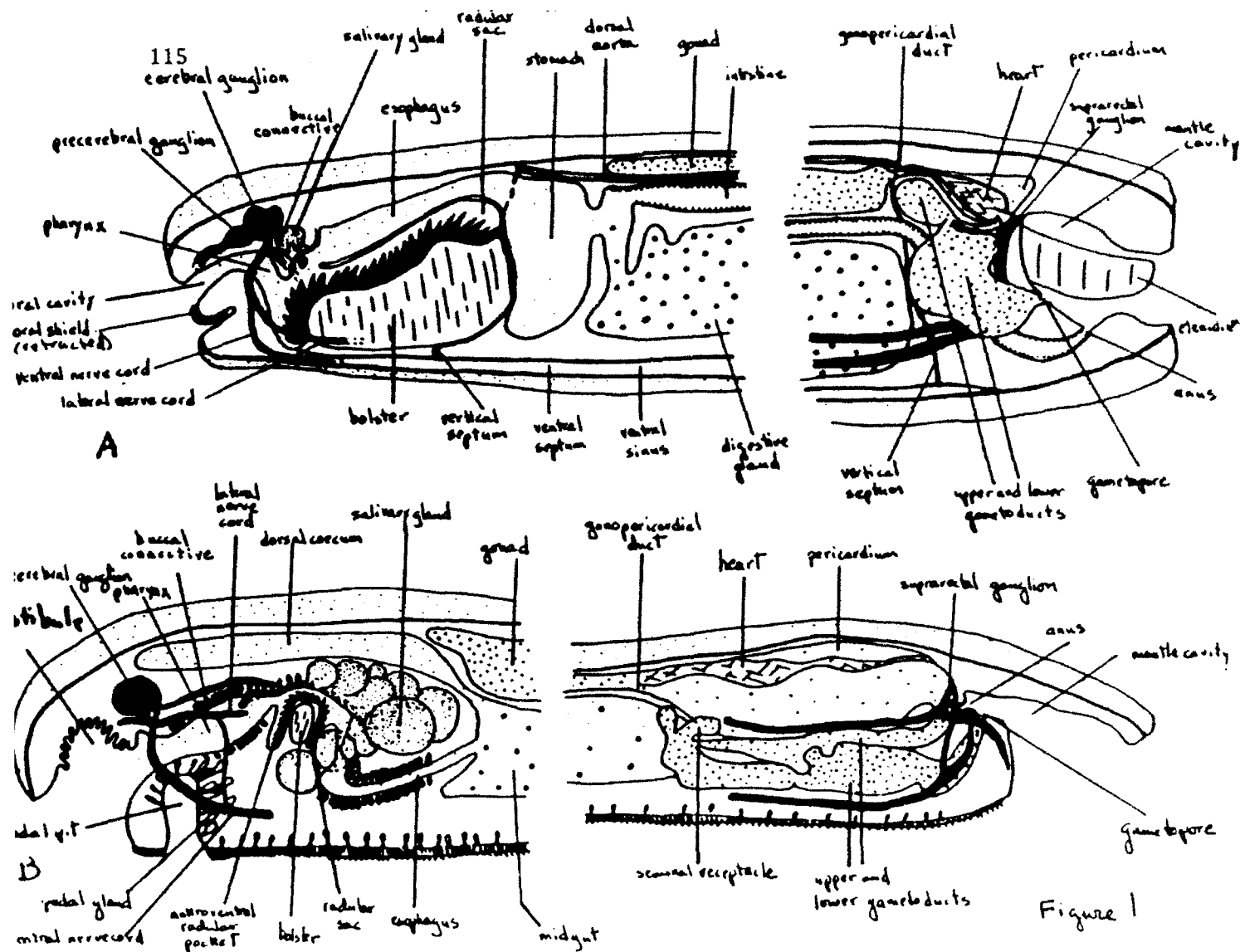


Figure 1

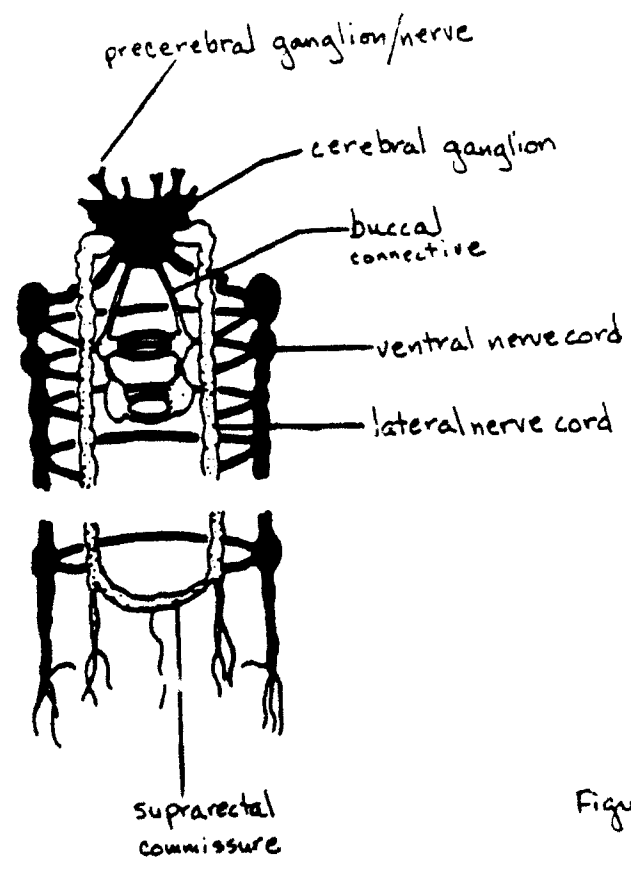


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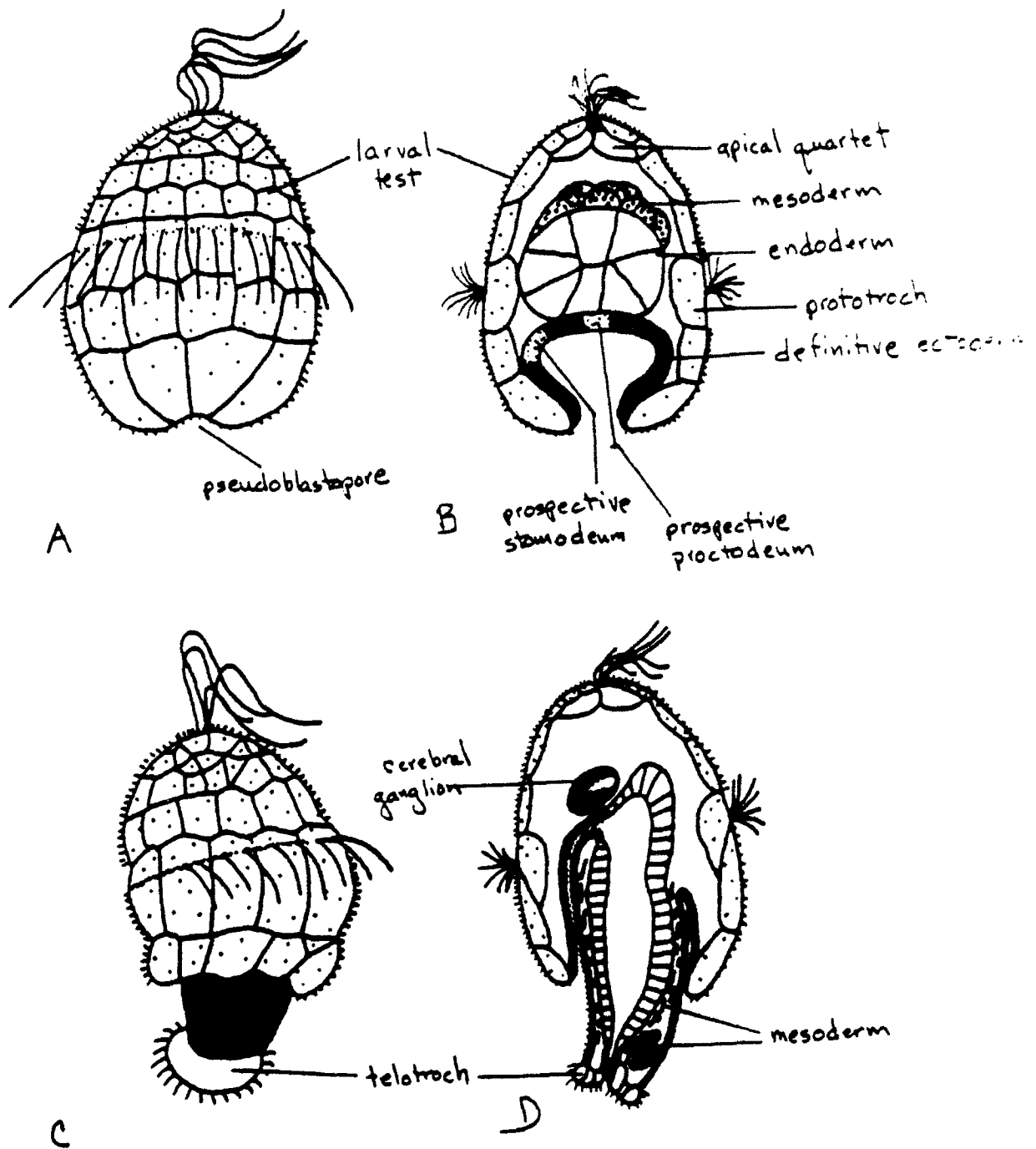


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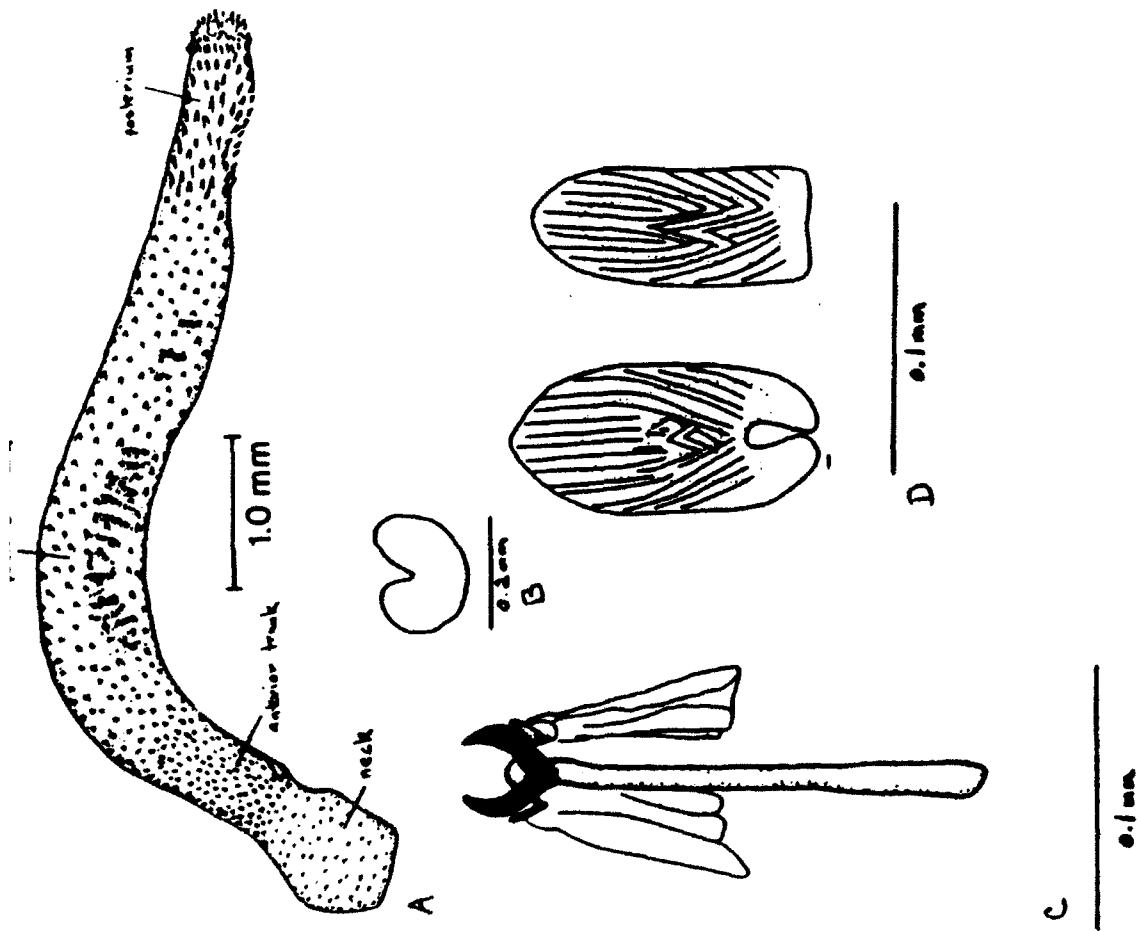


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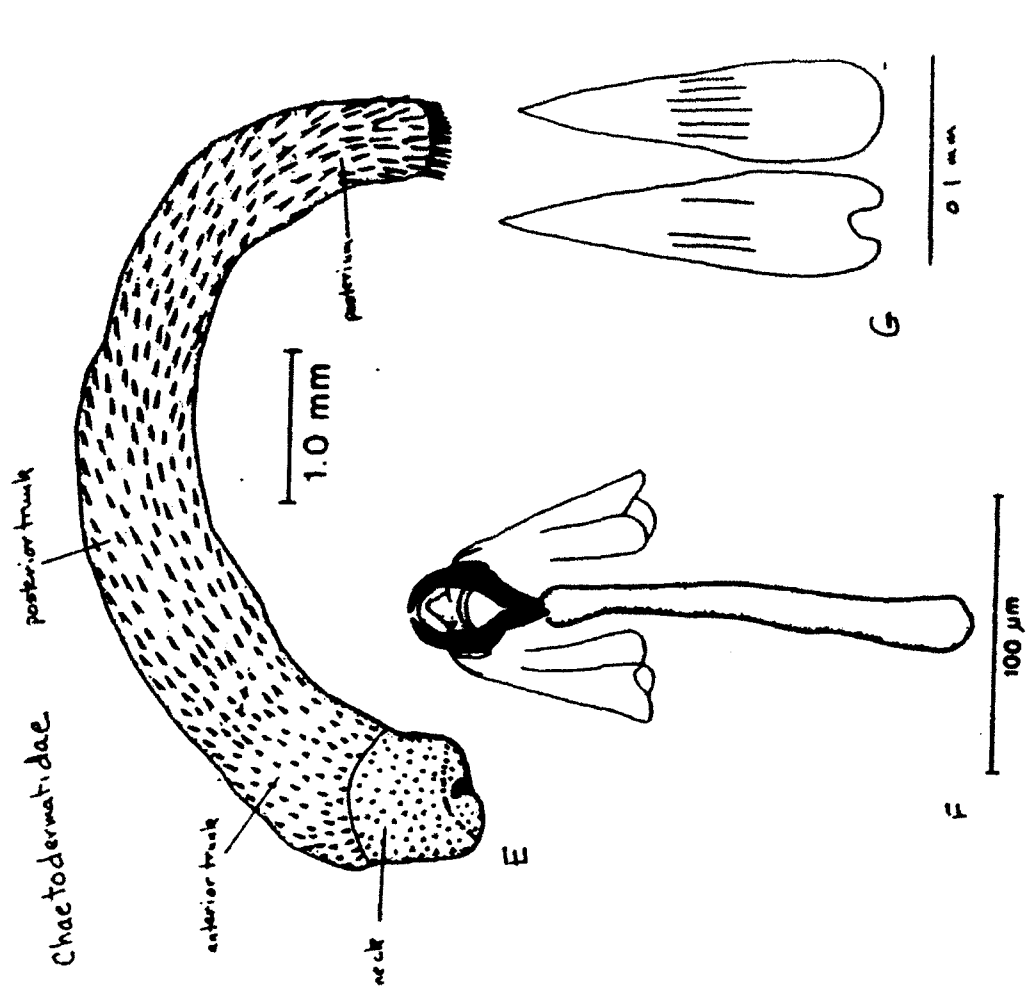
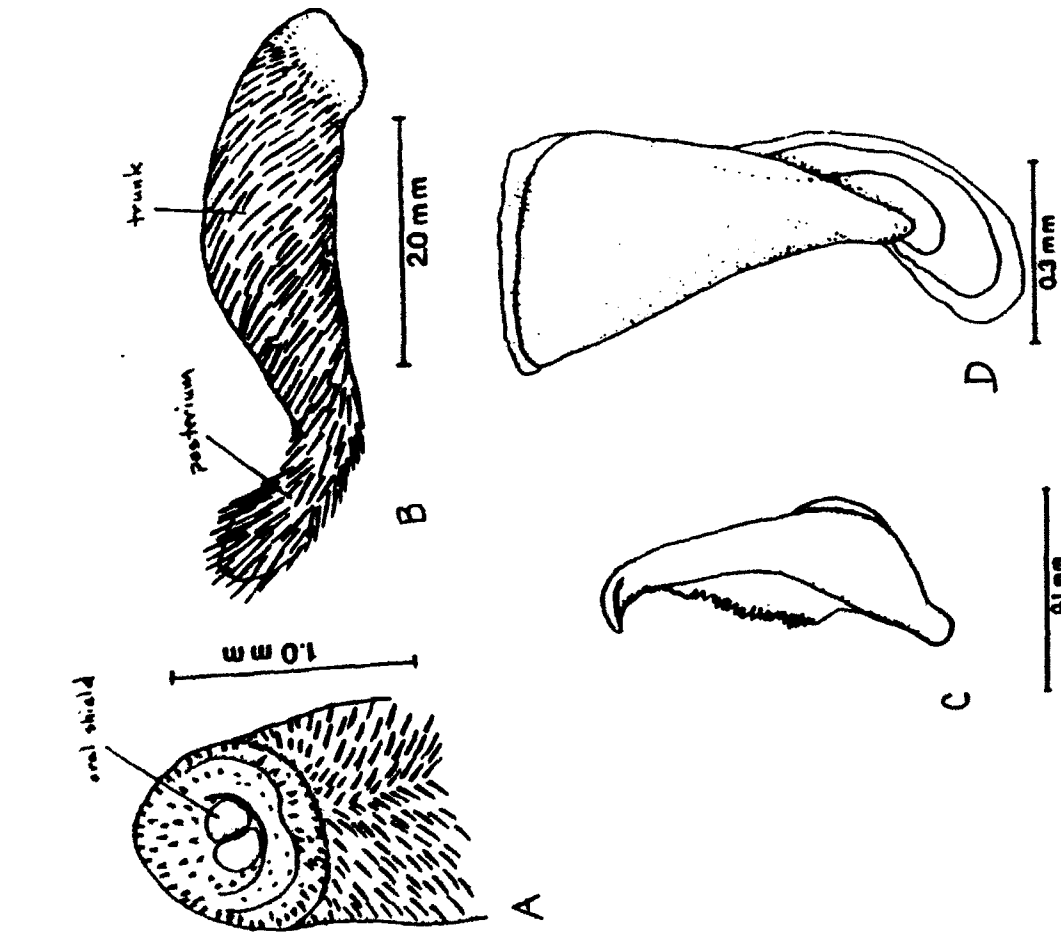


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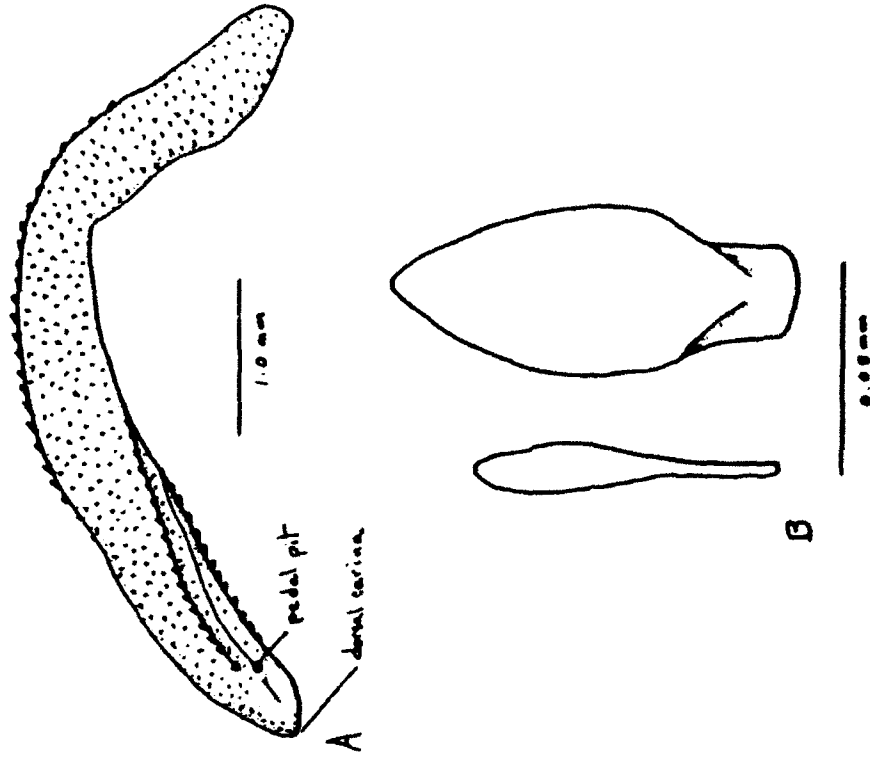
Prochaetodermatidae

Dondersiidae



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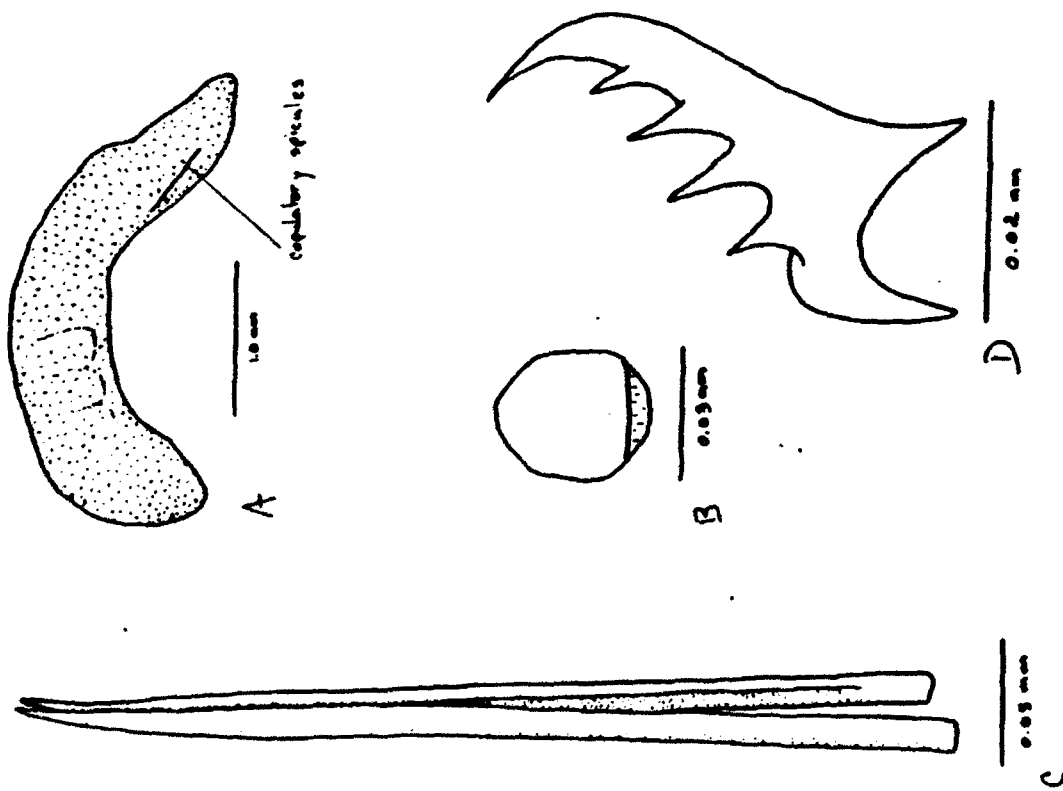
Figure 5



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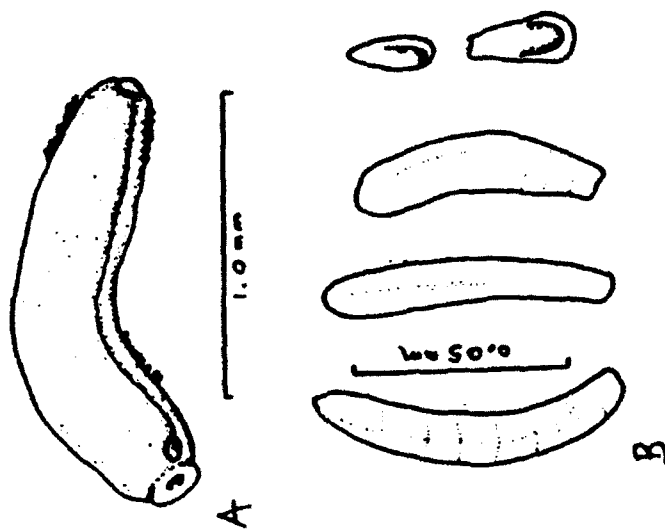
Figure 6

Lepidomeniidae



Single column

Figure 7



Notisomenia clarigena Thiele

Figure 8

Single column

## Neomeniidae

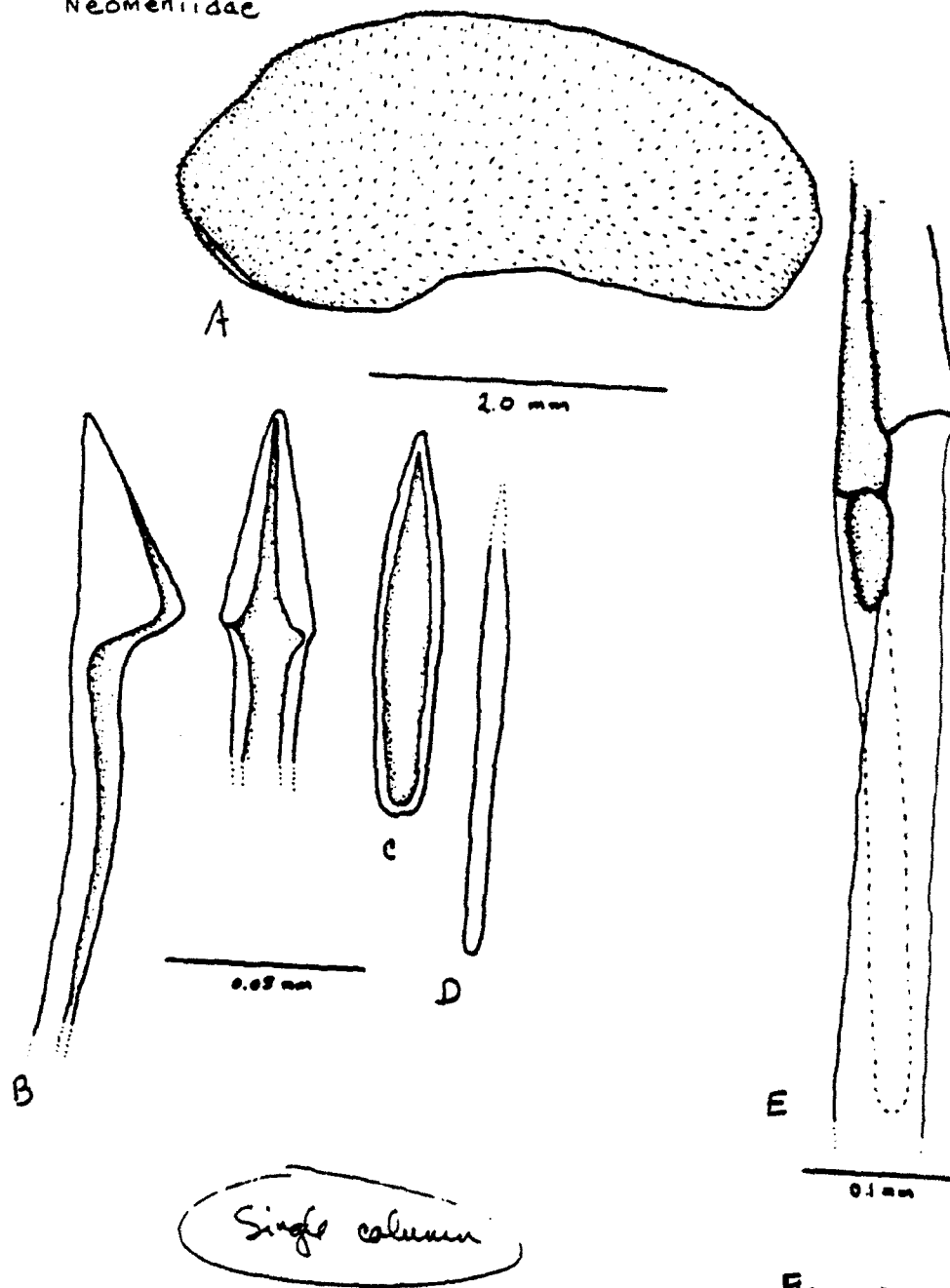
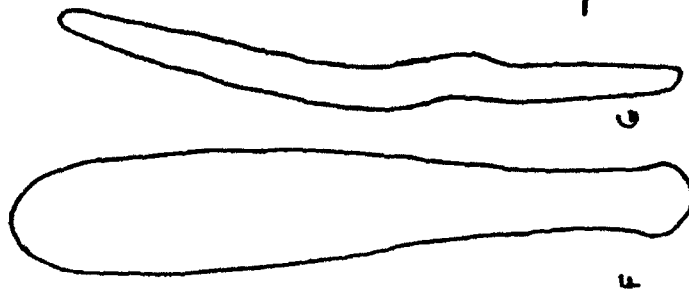
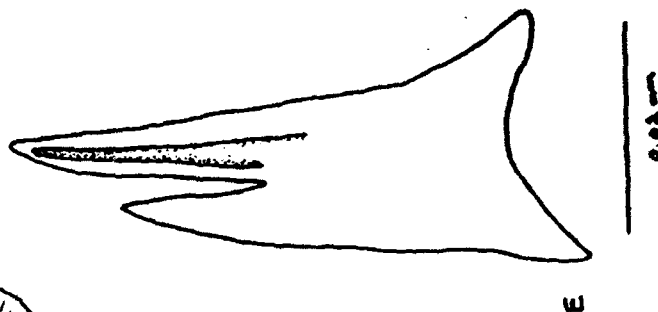
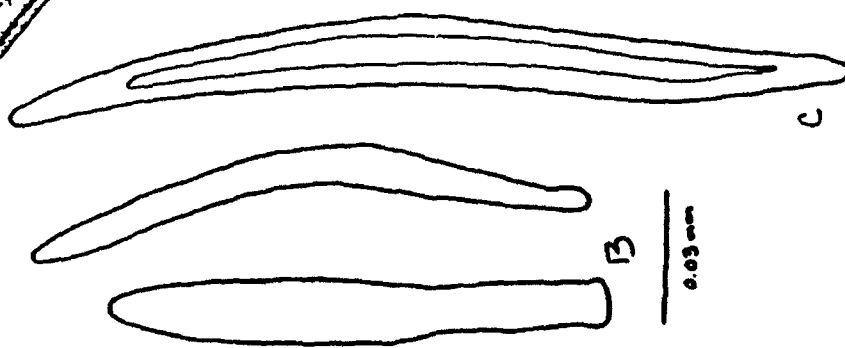
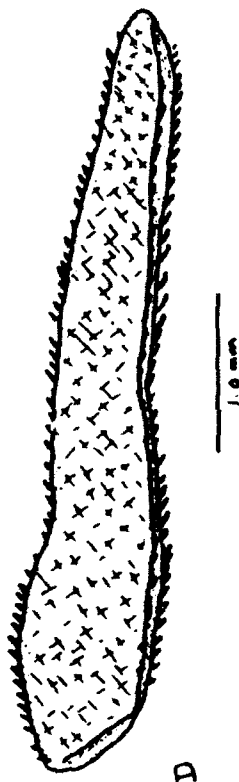
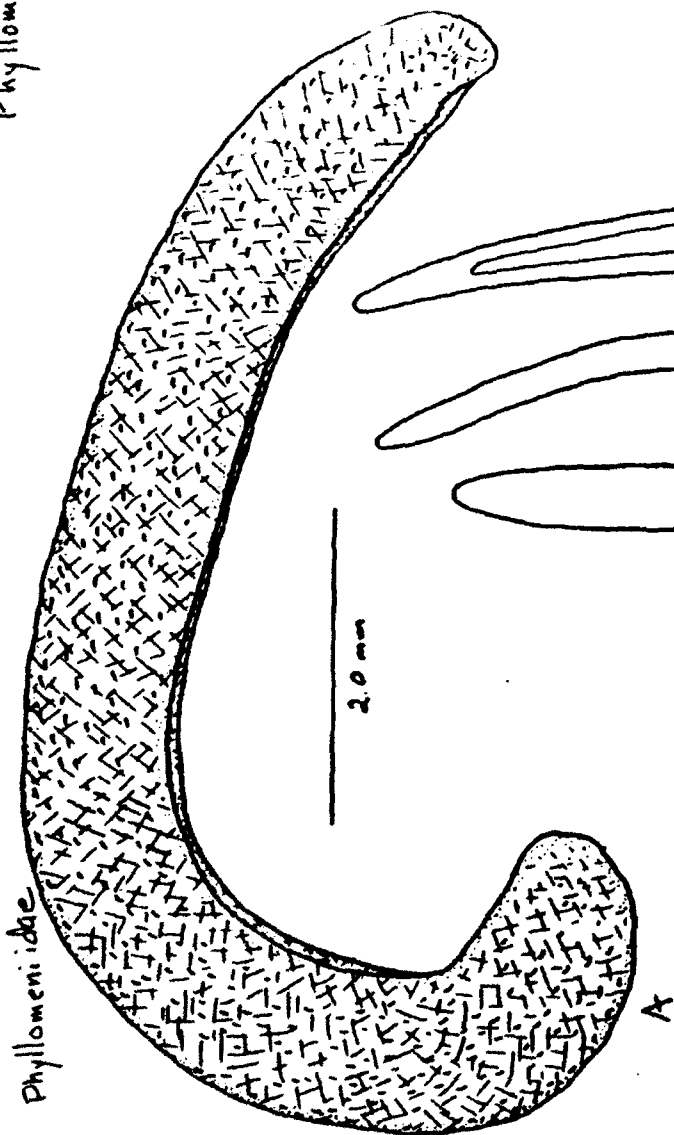


Figure 9



Phyllomeniidae



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Figure 10  
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Pararrhopalidae

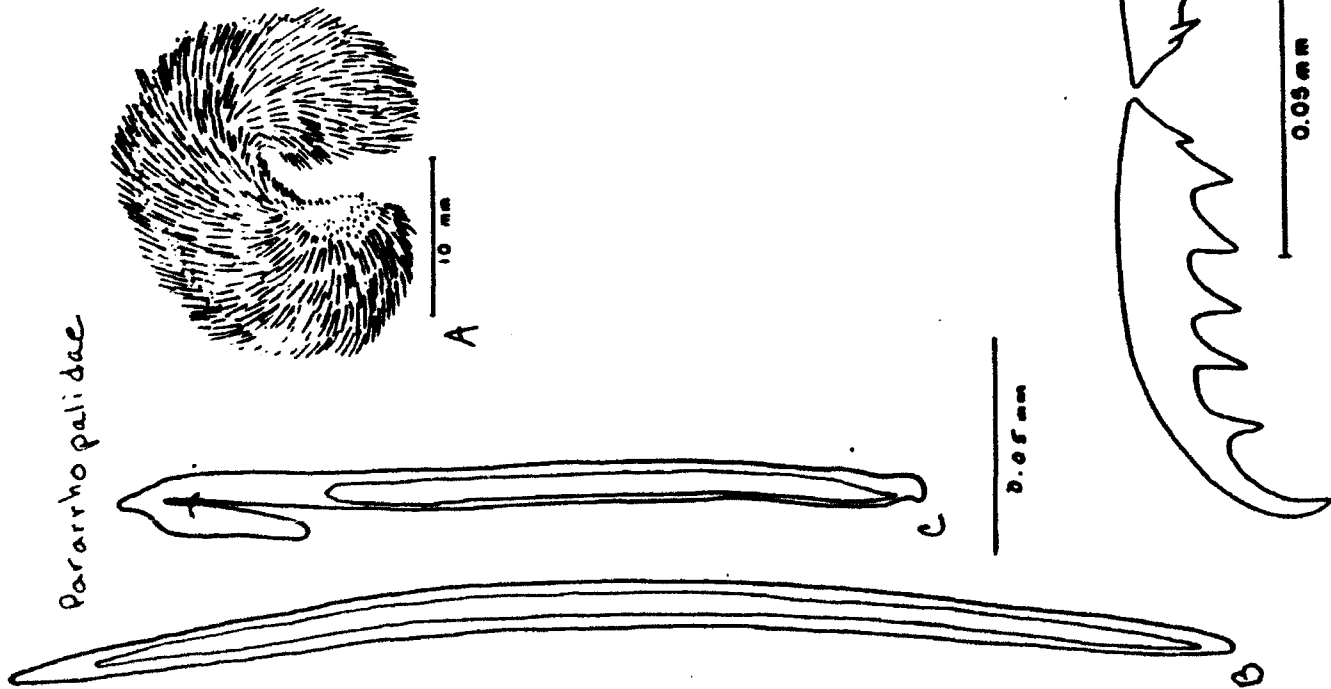


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## Proneomeniidae

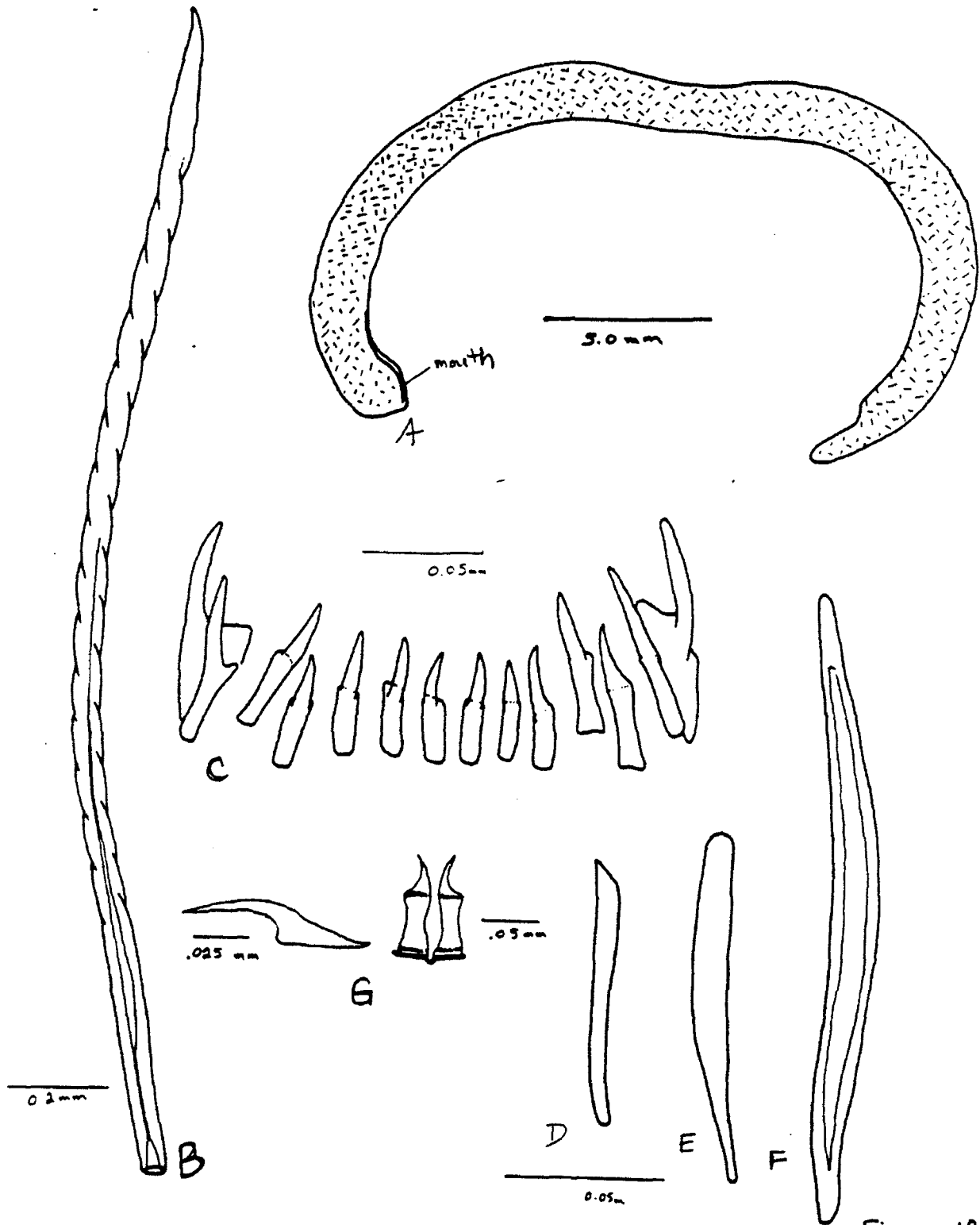
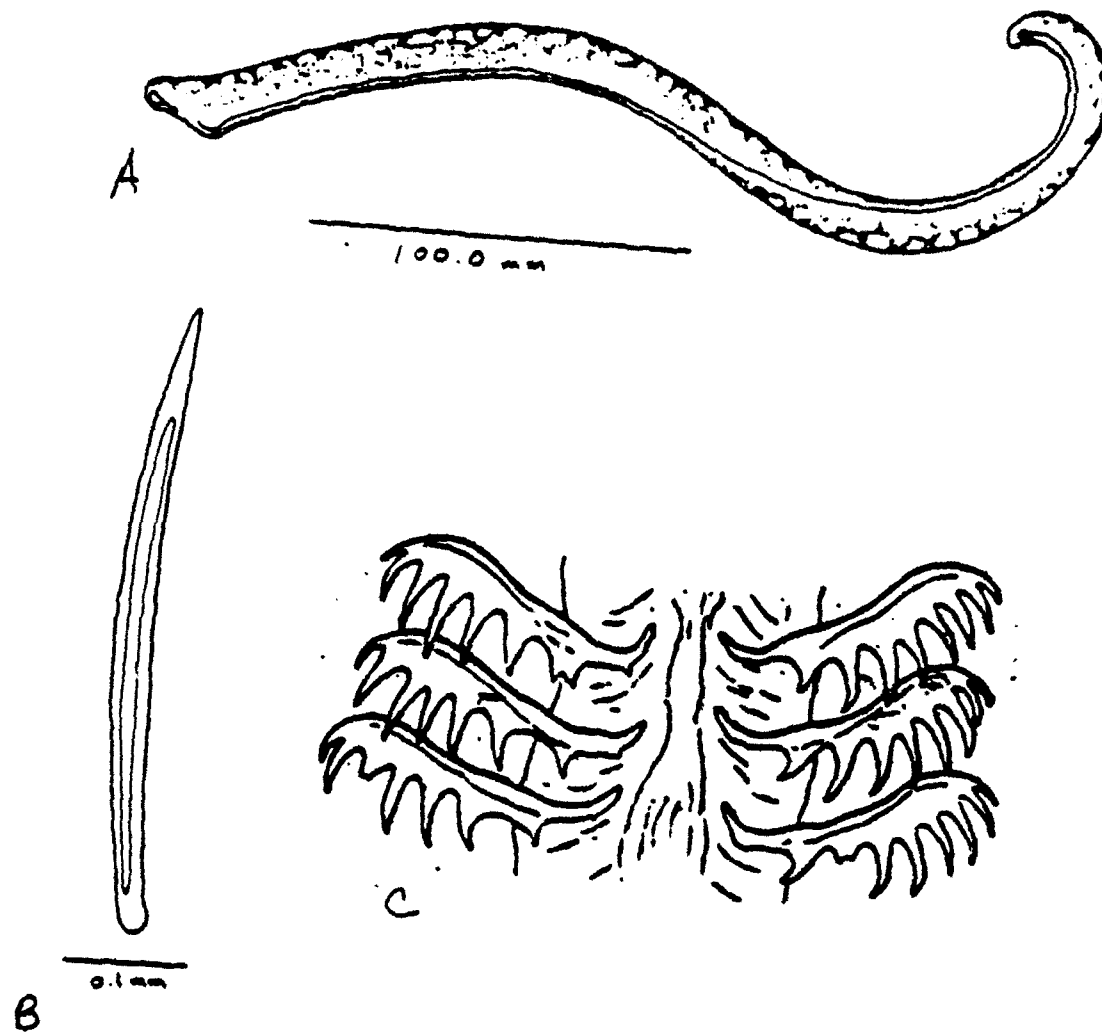


Figure 12

## Epimeniidae



Single column

Figure 13

**Aplacophora**

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<b>No. table:</b>	<b>1</b>
<b>Running head:</b>	<b>Aplacophora</b>
<b>Send proofs to:</b>	<b>Amélie H. Scheltema</b>
	<b>508/548/1400, ext. 2337</b>

## Introduction

The Aplacophora are specialized molluscs with a derived worm shape accompanied by reduction or loss of the foot and a small, reduced posterior mantle cavity. Their spiculate cuticular coat and internal anatomy, however, reflect a rather primitive molluscan state. Their phylogenetic relationship to other molluscs is not considered in this chapter which is only concerned with a descriptive anatomy of the class. (See Scheltema, 1988, and Salvini-Plawen, 1985, for contrasting phylogenetic views.) There are two groups: the subclass Neomeniomorpha (= Class Solenogastres *sensu* Salvini-Plawen) (Figs. 1, 3) and the subclass Chaetodermomorpha (= Class Caudofoveata) (Figs. 2, 4), here referred to as "neomenioids" and "chaetoderms," respectively.

## Material and Methods

Eighteen species, including new species and genera, supplied material for this chapter (Table 1), but many additional species inadequate for illustrative purposes were examined and provided supplementary information. Deep-sea material was fixed in formalin and preserved in 80% EtOH after screening and before specimens were sorted from the sample. Specimens for transmission electron microscopy (TEM) were sorted while still alive and fixed in glutaraldehyde. Specimens for light microscopy were decalcified in EGTA and embedded either in paraffin, sectioned at 7  $\mu$ m, and stained with Mallory-Heidenhain trichrome stain, or in Epon-Araldite, sectioned at 1.5  $\mu$ m, and stained with Richardson's stain (azure II and methylene blue). Specimens for TEMs first published here were decalcified in ascorbic acid or EDTA and embedded in Epon-Araldite or Spurr's low viscosity epoxy resin.

## General Anatomy

There are some major differences between the two subclasses of the class Aplacophora (Figs. 1-4). The creeping neomenioids retain a narrow foot in a ventral groove, which begins anteriorly as a pedal pit; the burrowing chaetoderms lack a foot. Chaetoderms possess a nearly or entirely circumoral sensory cuticular shield; the neomenioids have a papillate, sensory supra-oral vestibule. In chaetoderms the midgut is separated into a stomach and glandular digestive diverticulum; in neomenioids there is a single midgut organ combining stomach and digestive gland. Most neomenioids, but not chaetoderms, have serial sets of lateroventral muscle bands. Chaetoderms are dioecious, neomenioids are monoecious. In chaetoderms, but not neomenioids, there is a pair of ctenidia in the mantle cavity.

These differences aside, there are great similarities in mantle epithelium, body-wall musculature, foregut and radula, circulatory system, and, above all, ladderlike nervous system and reproductive system. The mantle is comprised of an epithelium and its secreted products, a cuticle and embedded calcareous spicules. Immediately beneath it, or separated by either a thin or thick dermis, lies a three-layered body-wall musculature. The gut passes from the anterior mouth to the posterior anus which lies in the mantle cavity. All Aplacophora are either carnivores or selective detritivores on organic material; many neomenioids feed on

**Cnidaria.** A radula is present with usual molluscan features of a radular sac and odontoblasts, radular membrane, and odontophore bolsters with their muscles to move the radula.

Posteriorly there is a heart lying in a spacious pericardium. Except for a dorsal aorta or sinus, circulation is open, and the internal organs are bathed in the blood of the hemocoel. A horizontal septum divides a ventral sinus from the rest of the hemocoel. The nervous system is comprised of a paired, usually fused cerebral ganglion from which arise two pairs of cords, the lateral and ventral, which are connected along their length by numerous cross-commissures. Posteriorly the lateral nerve cords end in a commissure above the rectum; in chaetoderms the ventral cords fuse with the lateral cords anterior to the suprarectal commissure. A pair of connectives leads from the cerebral ganglion to form a buccal ring. A dorsoterminal sensory organ, or pit, is found in nearly all Aplacophora. Other sensory structures are particular to the two major groups (e.g., oral shield and vestibule) or to lower taxa (e.g., additional sensory pits in the mantle).

The reproductive system in Aplacophora is unique among molluscs. The gonads pass into the anterior end of the pericardial cavity through a pair of gonopericardial ducts lying on each side of the dorsal aorta. Gametes pass through the pericardium to paired U-shaped gametoducts which lead to the mantle cavity. In neomenioids there are usually seminal receptacles and often copulatory spicules and seminal vesicles. The connection of gonads and pericardium may represent a primitive molluscan state as proposed by Goodrich (1945) or one derived as a result of a narrowed body. Salvini-Plawen (1970, 1985) suggests the latter on evidence from *Phyllomenia*.

Exocrine gland cells are abundant. Those of the epidermis perhaps have both an excretory and mucus-producing function. Glands or gland cells provide mucus to the oral shield area of chaetoderms and to the neomenioid foot and pedal pit. Salivary glands open into the pharynx near the radula. The epithelium of the digestive gland or midgut and gametoducts are mostly secretory; however, little is known about the function of these gland cells. Baba's paper (1940) on excretion and digestion in *Epimenia* remains the single account of experimental work done on a living aplacophoran.

Because so little has been published about function or, with the exception of the work of Haszprunar (1986, 1987) and Buckland-Nicks and Chia (1989), about the fine structure in the Aplacophora, the account which follows is not explicit about all the gaps in our knowledge. The many questions which are tacitly raised are worthy of further investigation.

### Epidermis

**Mantle** -- Epidermis that covers the body and bears a cuticle either with embedded spicules or without spicules on the lateral walls of the foot groove and in sensory pits, is considered to be mantle (Figs. 5, 6). The mantle epidermis has several cell types underlain by basement membrane and body-wall musculature. The most complete account of mantle epidermis is given in Hoffman (1949). Aplacophora share with Polyplacophora a similarity in papillar

epidermal structures and spicule secretion (see Salvini-Plawen, 1985, Figs. 36A-C [but not D, which is hypothetical], 37).

The organic cuticle appears to result from epidermal secretion (Figs. 5 A, 6 B, C; see also Rieger and Sterrer, 1975, Fig. 30); it is "composed of a glycoprotein complex with high acid mucopolysaccharide and low protein" (Beedham and Trueman, 1968). In chaetoderms it has a fibrous structure parallel to the body wall (Fig. 6 B, C). The thickness of both cuticle and epidermis varies among species, even those of the same body size or in the same genus (e.g., *Ocheyoherpia*). Cuticle thickness ranges from a few to several hundred microns, the latter occurring in some large species. There is no positive correlation between thickness of epidermis and cuticle (Fig. 5 C, F, G).

Epidermal spicules are aragonitic as determined by x-ray diffraction (Rieger and Sterrer, 1975; Scheltema, 1985) and are secreted extracellularly within an invagination of a single cell (Fig. 6 D) (Haas, 1981). The crystallization chamber of the calcium-carbonate secretory cell is sealed off by a collar of neighboring cells. Variations in shape, size, and thickness of spicules are of primary taxonomic importance. Spicules of the burrowing chaetoderms are solid and leaflike, triangular, spatulate, or rod-shaped, sculptured by ridges and grooves (Fig. 4 D). Besides possessing solid leaflike and rod-shaped spicules, neomenioid species also have solid or hollow spear-shaped, paddle-shaped, hooked, scooped, or S-shaped spicules (Fig. 3 C, D), and two or more spicule types are often present on an individual. In neomenioids the various spicule types are scattered over the entire body or lie in particular regions; in chaetoderms spicule type changes from anterior to posterior. Spicules are borne on the body from flat-lying to nearly erect. In some neomenioid groups one or more layers of skeletal spicules ("tangential" in older literature) lie within the cuticle at right angles to each other and diagonal to the longitudinal body axis (Fig. 5 C). Upright ("radial" in the older literature) and either flat-lying or skeletal spicules can exist together. There is great consistency in spicule morphology within a species.

The mantle epidermis has either a few or many large uni- or multicellular vesicles that extend into the cuticle and contain granular and other material; in species where they are stalked, they are referred to as "papillae" (Figs. 5, 6 B). More than one type of granule cell or papilla often occurs within an individual and can impart body color (Baba, 1940). Epidermal granule cells and papillae are thought, but not demonstrated, to be excretory cells because they appear to discharge their contents to the outside (Figs. 5 C, 13 E). In *Falcidens* they are seen to contain elements similar to blood cells (Fig. 6 B), and in *Helicoradomenia* long tubules with granules extend from the hemocoel into the epidermis (Fig. 5 B). Nerve and muscle fibers run through the body-wall musculature and end in the epidermis (Fig. 5 D, E). In most species the mantle epidermis rests directly on body-wall musculature; in some there is a thin or thick homogeneous dermis (Fig. 5 A) or layer of connective tissue (Fig. 6 B).

Mantle epithelium and its cuticle continues without spicules and with changes in cell type (1) to the base of, but not across, the dorsoterminal sense organ cleft, present in nearly all



Aplacophora (Fig. 15 D); (2) across the dorsofrontal sensory pit, present above the vestibule in some neomenioids (Fig. 10 A); and (3) along the lateral walls of the neomenioid footfold (Fig. 10 C, D).

**Vestibule** -- The neomenioids possess a vestibular chamber above the mouth, usually inaccurately called an "atrium" and presumed to be sensory (see below). The vestibule is lined by epidermis drawn out into a few or many, squat or slender papillae (Figs. 7 A, B, 8 A, B). The cells of the vestibular papillae are filled with secretory bodies and are provided with fibers from the underlying nerve and muscle nets. In *Aesthoherpia* a papilla in cross-section shows a thick microvillar border surrounding peripheral cells with a lucent cytoplasm containing electron dense single or coalesced granules; centrally there is a cortical cell and strands of nerve and muscle (Fig. 7 C) (Haszprunar, 1986). Ciliation of the vestibule varies from scarcely ciliated to bundles of dense, long cilia that border the mouth opening (Fig. 7 A).

**Oral shield** -- The epidermis surrounding the mouth opening in chaetoderms bears a thick, shieldlike oral cuticle (Figs. 4 A, B, 9 A). Mucous gland cells open peripherally through the cuticle; the mucus is contained in large vacuoles (Fig. 9 C). Sensory cilia penetrate the cuticle and reach the outside (Fig. 9 E, F). The oral shield cuticle is differentiated from both mantle and oral cavity cuticle, with which it is continuous, by a thick mass of microvilli underlying a dense outer border filled with dumbbell-shaped granules (Fig. 9 B, D).

**Foot and pedal pit** -- The greatly reduced neomenioid foot is usually formed of a single fold, or infrequently two, three, or several folds, that extend along the midventral length of the body within the cuticle-lined pedal groove of the mantle (Figs. 3 B, 10 C, D, 17 C). The blood space within the foot is hemocoel. The foot is heavily ciliated and provided with abundant mucous gland cells (Fig. 6 E). Muscle fibers are not evident within the footfold, and locomotion is by ciliary action of the expanded foot along a mucous trail (Salvini-Plawen, 1968a). Posteriorly, the foot ends just before or at the mantle cavity; anteriorly it joins a small to relatively large, protrusible pedal pit (Figs. 8 C, 10 B).

The pedal pit receives copious mucus from complex subepidermal pedal glands that fill much of the internal head region (Figs. 8 C, 10 E, 17 A). The pit is provided with very long, dense motile cirri; in *Aesthoherpia* each cirrus is comprised of 40 to 100 cilia and the epidermis is traversed by muscle fibers (Haszprunar, 1986). Free nerve endings are found between the epidermis and cilia in *Aesthoherpia*, and at each side of the pedal pit are long sensory cirri issuing from deep pockets (Fig. 10 F, G).

**Mantle cavity** -- The epithelium of the mantle cavity wall is either ciliated or has a microvillous brush border, and there are usually abundant gland cells of various types (Figs. 11 E, 12 C). In *Neomenia carinata*, bacteria are found associated with the brush border and are engulfed by mantle epithelium (Fig. 11 E). Near the entrance to the mantle cavity the

epithelium often bears long cilia and has large gland cells that differ from those found proximally (Fig. 12 D). In many neomenioids, large subepithelial gland cells lie above the mantle cavity and open into it. The mantle cavity is usually closed by muscles in preserved specimens (Fig. 3 B).

The paired respiratory gills of the chaetoderms are true molluscan ctenidia with afferent and efferent channels along a muscular gill axis, which gives off alternating ciliated lamellae which produce a dorsal to ventral current (Fig. 11 A, B) (Salvini-Plawen, 1985). The positions of efferent and afferent vessels, however, are dorsal and ventral, respectively. Ctenidial epithelium is polyciliated with many apical mitochondria (Fig. 12 A). Ctenidial tips, with fewer cilia, contain large gland cells and there are dark lamellar structures between the microvilli (Fig. 12 B). The ctenidia are supplied with nerves. Normally they extend outside the mantle cavity (Fig. 4 C) but can be withdrawn by means of three pairs of retractor muscles. The respiratory structures of neomenioids are simple extensions of mantle cavity epithelium thrown into low or high plicated folds or papillae (Fig. 11 C, D). Papillae bear cirri and contain gland cells and blood lacunae (Fig. 11 F).

In neomenioids, deep anterior mantle cavity pockets are often present that are associated with the reproductive system (q.v.).

### Body-wall and lateroventral musculature

Fully expressed body-wall musculature consists of three muscle layers: an outer circular band, a middle oblique layer with two orthogonal bands, and an inner longitudinal band (Figs. 13 B, D, 20 G). Depending upon the taxon, one or more layers may be lacking (Figs. 6 A, B, C, 13 G). Ventral longitudinal muscles are thickened on each side of the foot groove in neomenioids, often becoming discrete bands (Fig. 13 B). Contraction of these muscles gives neomenioids their distinctive crescent shape and generic suffix (*-menia* = moon). In some chaetoderm groups the longitudinal muscles break up into four heavy bands of large bundles (Fig. 13 G). The body region in which these bands lie is distinctly narrower than the rest of the body (Fig. 4 A). Muscle-fiber bundles in both groups are surrounded by a thick connective tissue matrix (Figs. 6 B, C, 13 A, G). Anteriorly a thickened band of circular muscles in many chaetoderms forms a constriction to which attach the numerous bands and fibers that move the mobile head region (Fig. 4 A, B). Locomotion in chaetoderms occurs through hydrostatic elongation and forward movement of the head region followed by contraction of the longitudinal muscles.

Two serial sets of lateroventral muscles occur in most neomenioids (Fig. 13 B, C). The more dorsal pair runs from the lateral body-wall muscles to the mantle epidermis of the foot groove and interrupts the midgut which pouches out between them. The more ventral pair runs from body-wall muscles to become the horizontal muscle layer, or septum. Fibers from the more dorsal pair also join the horizontal septum. In *Aesthoherpia* the septum is bound by a compact, 200 nm thick lamina (Fig. 16 E) and contains nerve fibers from the ventral ganglia as well as connective tissue (Haszprunar, 1986). The lateroventral muscles apparently

serve to close the foot groove and to regulate the volume of blood in the foot.

### Hemocoel and circulation

A heart consisting of a ventricle and usually paired auricles lies within a spacious pericardium (Figs. 22 A, B, 23 F). A muscular aorta or a thin-walled dorsal sinus leads anteriorly from the ventricle and empties into the hemocoel of the anterior end (Figs. 3, 4, 8 A, C). A muscular aortal bulb may also be present (Fig. 22 A). The heart is formed from an invagination of the dorsal pericardial wall (Figs. 14 A, 22 C) and is either wholly or partially suspended by a membrane from the pericardium or is open partially or completely to the dorsal sinus. Muscle fibers strongly or weakly criss-cross the ventricle. The auricles are usually less muscular than the ventricle and fuse before entering it posteriorly through an often muscular single or paired auriculoventricular opening. The ventricle wall in chaetoderms is strongly folded and numerous mitochondria are present, evidence of transport epithelium, although there are no specialized structures (Fig. 14 A, B, C).

Blood passes posteriorly into the auricles presumably after respiration in the ctenidia or gill folds. Blood is gathered either from a sinus at the base of the efferent channels in chaetoderms (Fig. 22 A) or, in neomenioids, from a posterior dorsal sinus (Fig. 11 C) or directly from the hemocoel (Fig. 22 C). Heart pulses of 19 to 37 beats per minute have been recorded (Salvini-Plawen, 1968a, b). Other than the dorsal aorta, blood vessels are lacking except for a pair of short tubes leading from the hemocoel to the radular apparatus in some species (e.g., *Chaetoderma*, Scheltema 1972). The hemocoel is divided by the ventral horizontal muscle layer, or septum, which defines a ventral, or pedal, sinus whether or not a foot is present (Figs. 13 B, G, 16 C, E). Anterior or posterior vertical septa are found in some chaetoderms (Fig. 2 A, B).

Two or more types of blood cells can usually be distinguished in fixed material (Figs. 13 F, 14 D), and Baba (1940) demonstrated three cell types in living *Epimania*: amebocytes, erythrocytes, and disc-shaped platelets. The presence of empty blood cells in the hemocoel and of material similar to that in blood cells within epidermal papillae suggests that excretion can occur through the outer body wall (Figs. 5 B, 6 B, 13 E), although injection experiments by Baba (1940) using carbon particles and carmine dye with *Epimania* were negative. His experiments demonstrated that amebocytes were discharged through the epithelium of the midgut, rectum, and mantle cavity.

### Nervous system and sensory elements

Nervous system -- The fused cerebral ganglion and the ganglia of the lateral and ventral cords are composed of large bundles of centrally located internal axons with peripherally located nuclei (Figs. 6 A, 8 C, 15 A, B, C). A distinct connective tissue cover encapsulates the ganglia and cords (Fig. 15 C). In the cerebral ganglion of *Chaetoderma* many glial membranes interdigitate and isolate the major axonal bundles (Fig. 15 A). Frontally there are three or more pairs of cerebral swellings or precerebral ganglia which give off numerous

nerve fibers to the mouth and vestibule or oral shield (Figs. 1 C, 2 A, 7 B, 9 E, F). Differences in the nervous system between neomenioids and chaetoderms appear to be related to locomotion, with greater fusion of nerve components occurring in the burrowing, footless chaetoderms. In neomenioids, the ventral and lateral cords remain separated (Fig. 17 C) after arising usually independently from the cerebral ganglion (Fig. 1 C), whereas in chaetoderms the cords arise from a single pair of connectives, run next to each other for most of the body length, and fuse posteriorly (Figs. 2 A, B, 13 G). In neomenioids the anterior pair of ventral ganglia, which give off nerves to the pedal pit and pedal glands (Salvini-Plawen, 1985), are larger than the more posterior ones (Fig. 1 C).

Nerves from the lateral cords extend to the mantle epithelium (Fig. 5 D) and internal organs; in *Scutopus* they are most numerous anteriorly (Salvini-Plawen, 1985), where the heaviest longitudinal muscles used in burrowing are located. In neomenioids there are many commissures between the ventral ganglia which innervate the pedal groove, but there are few in chaetoderms.

The suprarectal ganglion innervates the mantle cavity and receives sensory input from the dorsoterminal sense organ in both groups (Fig. 22 C). In chaetoderms, it also innervates the ctenidia (Salvini-Plawen, 1985).

Sensory elements -- A sensory organ lies dorsally near the mantle cavity opening. It is a protrusible pit or groove of mantle epithelium covered over by spicules and lined on the sides by cuticle (Figs. 15 D, E, 16 A) (Pruvot, 1891; Haszprunar, 1987). The cuticle of this dorsoterminal sense organ is covered by a protective mucous layer. A distinct or fine basal lamina and circular muscles underlie the organ. Multiciliated sensory cells with parallel laminae are open to the surrounding medium (Fig. 15 D), and in *Chaetoderma nitidulum* collar receptors are present (Fig. 15 E). Some species have more than one dorsoterminal sense organ. Haszprunar (1987) conjectured that dorsoterminal sense organs are chemoreceptors and may be used in reproductive activity. Their conjectured homology to the osphradium, however, remains to be demonstrated.

A protrusible dorsofrontal pit, presumably sensory, lies above the vestibule in some groups of neomenioids. It is furnished with cells whose distal borders appear to bear sensory cilia (Fig. 10 A).

A nerve net 20 to 30  $\mu\text{m}$  thick with many ganglia underlies the vestibular papillae in *Aesthoherpia* (Haszprunar, 1986). The nerve net gives off thin processes that run both as free nerve endings to the surface of the vestibular epithelium and up through the central core to the tips of the papillae (Fig. 7 C). These neural processes bear one or a few short cilia without basal rootlets or central microtubules.

Stiff frontal stereo-cirri underlain by a nerve plexus rim the vestibule in several neomenioids (Haszprunar, 1986; also called oral setae, atriobuccal cirri). The cirri in *Aesthoherpia* consist of many macrocilia, each with a long, broad shaft with up to 48

randomly arranged double and one or more single microtubules. In front of the pedal pit in *Aesthoherpia* are two anterolateral, long cirri whose cilia resemble those of the frontal cirri except that the basal bodies lack rootlets (Fig. 10 F, G). Each cirrus sits in a pocket adjacent to muscle and is surrounded by nerve tissue.

The sensory oral shield of chaetoderms is described above and in Figure 9 E, F.

Unique bell-shaped receptors occur in the pedal pit and ciliary region of the foot groove in *Aesthoherpia* (Fig. 16 D) (Haszprunar, 1986). A single cilium within the receptor has a very short rootlet and shaft and an outer membrane inflated into a conical shape.

In several neomenioid genera, a hollow space bordered by a thick basal lamina and an envelope of loose tissue is situated anteriorly between the large anterior ventral cord ganglia and below the ventral septum and pedal commissure (Fig. 16 C, E). Loose within the lumen are cells which have dense nuclei with thin peripheral cytoplasm surrounding large vacuoles containing light refractive inclusions. In *Aesthoherpia* the basal lamina is joined to the lamina of the ventral septum (Fig. 16 E) (Haszprunar, 1986). Thick nerves run from the ventral ganglia to the anterior wall of this so-called "pedal commissure sac," the fibers penetrating the cells of the envelope. In *Gymnomenia* the hollow space contains calcareous bodies that appear to be statoliths (Scheltema, 1981), but their composition in *Eleutheromenia* (Fig. 16 C) has not been determined. A locomotory receptor is conjectured to be their function (Haszprunar, 1986).

### Digestive system

Mouth opening and oral cavity -- The mouth opening is closed by a sphincter muscle. It is entirely or partially surrounded by the oral shield in chaetoderms (Fig. 9 A) and in neomenioids it is situated either at the proximal end of the vestibule (Fig. 7A) or is separate from it. The mouth opens directly into an oral cavity ("oral tube," Scheltema, 1981; "buccal cavity," Salvini-Plawen, 1985) whose epithelium may be folded, nearly smooth, ciliated, or cuticularized (Figs. 8 C, D, 21 A). Goblet cells are present, and in many neomenioids there is a dorsal so-called gland presumed to be salivary. In chaetoderms, the epithelial cells change abruptly from the type found beneath the oral shield (Fig. 9 D). There are often sensory cirri in the oral cavity of neomenioids similar to those of the vestibule (Figs. 8 D, 16 B, 21 A). A pair of strong retractor muscles runs posteriorly and laterally from the proximal end of the oral cavity in both neomenioids and chaetoderms, and a strong sphincter separates the oral cavity from the pharynx, which is dorsal to it (Figs. 1 A, 17 A).

The oral cavity epithelium indicates secretory and sensory functions. In species where the pharynx is protrusible, it passes through the oral cavity, and the mouth opening may then be said to lie at the sphincter between the oral cavity and pharynx.

**Pharynx and esophagus** -- The epithelium of the pharynx ("buccal cavity," Scheltema, 1972, 1981) may be similar to that of the oral cavity or quite distinct. It is cuticularized, often heavily so, and is usually encircled by muscle fibers. Ventrally there is a radular sac (Fig. 17 C) with a large or small radula, although in about 20 percent of neomenioids the radula is lacking, in which case the pharynx is provided with sets of strong circular muscle bands and probably acts as a suctorial pump. Profuse secretions are provided to the pharynx by numerous individual gland cells and by the nearly ubiquitous paired ventral salivary glands (Figs. 13 B, 17 F, 20 A, B). These structures vary considerably. Individual gland cells may occur as goblet cells scattered in the epithelium or as dense masses of subepithelial cells (e.g., *Genitoconia*, Salvini-Plawen, 1967). The paired multicellular salivary glands, ventral to lateral in position, or occasionally dorsal, are simple in nearly all species (see Welsch and Storch, 1973 for terminology). Each opens through a usually tubular duct where the radular sac opens into the pharynx (Fig. 20 A), but in some species the terminal end is acinar (e.g., *Alexandromenia*, Heath, 1911). There are a few instances of intraepithelial glands (Fig. 20 B) or of compound glands (e.g., *Spengelomenia*, Heath, 1912). In *Scutopus* the fibrous-appearing vacuoles of the salivary gland cells are situated between small areas of cytoplasm with microvilli (Fig. 17 F). In most neomenioids the salivary glands show a strong basophilic reaction to trichrome stain. A short or long esophagus is sometimes present between the pharynx and midgut (Figs. 2 A, 17 C). The esophageal epithelium is often just an extension of pharyngeal epithelium, but it may be distinctive (e.g., *Limifossor*, Heath, 1905).

**Radula** -- The aplacophoran radula consists of either a single or a fused paired radular membrane which bears from a few to more than 40 rows of monostichous, distichous or polystichous cuticular teeth (Fig. 18) (Scheltema, 1988; Scheltema et al., in press). The distichous form is the most primitive. The radula is secreted proximally in a radular sac (Fig. 17 D) and migrates forward. Numerous odontoblast cells with basal nuclei indicate their secretory activity distally by dark-staining fibers; they produce the bases of the teeth. The radula becomes broader as it lengthens, and denticles are added medially (Scheltema, 1988). Abutting the odontoblasts are darker-staining membranoblasts with medially placed nuclei. They produce the radular membrane, which stains differentially from the attached teeth (Figs. 17 D, 18 C, 19). The superior epithelium secretes the denticles and possibly adds tanning proteins, for distal teeth are stronger than those just formed, and in chaetoderms they become yellow to brown in color. Anterior to the membranoblasts the inferior epithelium upon which the radular membrane rests has a brush border (Fig. 19).

In most chaetoderms, the distal teeth emerge from the radular sac into the pharynx. In neomenioids, the teeth exposed in the pharynx are usually not distal but are in the middle of the radula, which then bends ventrally and passes into a single or paired blind ventral pocket (Figs. 13 B, 18 E). Here the oldest teeth are either held and eventually dissolved, or they are retained and thus the entire ontogenetic history of the radula can be determined.

In the hemocoel beneath the radula is the odontophore with paired bolsters (Fig. 17 C), which are formed either of interwoven fibers of muscle and probably collagen (Figs. 17 E, 19) or of large empty-appearing cells with small nuclei, putatively chondroid tissue, to which

muscle bands are attached (Fig. 17 B). Muscles that move the radula include a number of protractors and retractors; which have been described for a few species (*Limifossor*, Heath, 1905; *Scutopus*, *Chaetoderma*, Deimel, 1982; *Genitoconia*, Salvini-Plawen, 1967). With the exception of the family Prochaetodermatidae with jaws and specializations for rasping (Scheltema, 1981), the radular teeth show no wear in Aplacophora and the radula may serve primarily as a rake or internal food transport device. Most neomenioids are provided with at least some circular pharyngeal muscles and are assumed to suck up the coelenterate tissue upon which most of them feed. In the family Chaetodermatidae, the derived cone-like radula with a single pair of denticles provides pincers for selective carnivory (Fig. 18 B).

**Midgut** -- The stomach in chaetoderms is separate from a ventral, blind digestive diverticulum, but in neomenioids the stomach and digestive gland cells are combined in a single midgut organ that often extends anteriorly into a single or paired midgut dorsal cecum (Figs. 8 C, 17 C). Common to most species in both groups is a ciliated fold, band, or groove which runs dorsally down either the stomach or midgut and leads to the ciliated intestine; it appears to function as a dorsal typhlosole (Scheltema, 1981).

Epithelial cells of the chaetoderm stomach are low and homogeneous, containing droplets and granules (Fig. 21 C). At the base of the stomach in the derived genera *Chaetoderma* and *Falcidens*, there is a gastric shield beneath which a mucoid rod turns in a style sac at the anterior end of the intestine (Fig. 20 C, D). These structures are lacking in the other, more primitive chaetoderm genera. The digestive diverticulum opens from the posterior end of the stomach. It has two types of digestive cells which are uniform throughout the chaetoderms, with the exception of the Prochaetodermatidae (Scheltema, 1981). Cells lining the dorsal side are packed with mineralized granules which have concentric dark layers and are membrane-bound (Figs. 20 D, 21 D, E). Laterally and ventrally the cells have a large apical vacuole, a small lateral or basal nucleus, and numerous mineralized granules (Figs. 20 D, 21 F). Within the vacuole lies a basophilic glandular body which is released by cell rupture into the lumen of the digestive diverticulum. Among neomenioids there is no such homogeneity of digestive cell types and there are various inclusions within the digestive cells (Fig. 20 E, F, G). Most neomenioids feed on cnidaria and are, perhaps, prey-specific (Fig. 21 B). Baba (1940), experimenting with living *Epimenia*, reported both extra- and intracellular digestion, and noted that nematocysts were rarely ingested but remained intact within the midgut lumen. In chaetoderms, food particles are not found in the digestive gland.

**Intestine** -- The epithelium of the intestine and rectum consists of simple cuboidal or columnar cells with granules and long cilia (Fig. 22 C). In chaetoderms the intestine is long. It begins with one or two bends at the posterior end of the stomach or style sac, if present, and passes with its formed fecal pellets dorsolaterally, to finally bend ventrally and open into the mantle cavity between the ctenidia. The neomenioid intestine is short, leading from the posterior end of the midgut to empty into the mantle cavity either above or below the single or paired gametoduct openings. In living *Epimenia* both excretory products, including blood cells, and undigested food, including nematocysts, are discharged (Baba, 1940).

### Reproductive system

**Reproductive tract** -- The gonads lie mid-dorsally in both the dioecious chaetoderms and hermaphroditic neomenioids (Fig. 13 C). They are paired in adult neomenioids and juvenile chaetoderms, but become fused in the latter as adults (Scheltema, 1973). The gametes pass through usually paired, narrow, ciliated gonopericardial ducts to the large pericardium (Figs. 1 B, 2 B, 14 A, 22 D, 23 F, 24 F-I), which bears paired, lateral ciliated tracts leading posteriorly to the openings of paired upper gametoducts (Fig. 22 C, D). The upper gametoducts usually bend and lead anteriorly before again bending to join the larger, lower gametoducts, which run posteriorly and empty into the mantle cavity. The gametopores are paired in chaetoderms, but in most neomenioids the lower gametoducts unite and empty through a single gametopore (Figs. 11 B, 23 E). In female chaetoderms, the mantle cavity epithelium adjacent to the gametopores forms ciliated tracts lined by mucous cells.

The reproductive tract of chaetoderms is simpler than that of neomenioids both in variety of cell types and in lack of accessory structures. The epithelium of the upper gametoducts is formed by simple cuboidal, multiciliated cells, while that of the lower gametoducts has enlarged, highly vacuolated cells with a complex basal membrane labyrinth (Figs. 6 A, 23 G). The upper gametoduct in neomenioids is formed of a homogeneous, ciliated epithelium; there are often seminal vesicles for the storage of endogenous sperm (Figs. 22 E, F, 24 G, H). Sac-like or lobed seminal receptacles for exogenous sperm storage usually open from the lower gametoducts close to their junction with the upper gametoducts (Figs. 22 F, 24 F-I). The epithelium of the lower gametoducts varies widely among species, but the cells are almost always high columnar and glandular, at least after the gametoducts unite, and may not be homogeneous (Figs. 22 E, 23 A, B). In *Gymnomenia*, spermatophores are contained in the lumen (Fig. 23 B).

Besides a more elaborate reproductive tract, many neomenioids have paired single or grouped calcareous copulatory spicules, which are held in deep pockets of the mantle cavity (Figs. 22 F, 23 A, C-E, 24 A-E). Glandular epithelium forms copulatory spicule glands, which may be large (Figs. 23 A, D, E, 24 H), and accessory copulatory spicules may lie at the edge of the mantle cavity (Figs. 11 C, 24 C, E). Other mantle cavity pockets may serve as tubular extensions to gametopore openings (e.g., *Dorymenia*, Salvini-Plawen, 1978) or as brood pouches (e.g., *Halomenia*, Heath, 1911). The reproductive anatomy suggests internal fertilization.

**Gametes** -- Oocytes are large and yolk-filled, often with two or more nucleoli (Fig. 23 H). The nuclear membrane dissolves by the time mature ova have reached the pericardial cavity (Figs. 22 D, 23 F; Scheltema, 1987). In neomenioids, oocytes are usually formed from cells of the medial gonadal walls and spermatozoa from the lateral walls. Chaetoderm spermatozoa are considered primitive, possessing an acrosome, an ovoid-shaped head, a short mid-piece with 5 mitochondria arranged symmetrically around two perpendicularly placed centrioles, a centriolar satellite complex that anchors the distal centriole to the plasma membrane through an annulus, and a short flagellar tail with a tapered end-piece containing



only the 2 central microtubules (Fig. 25 B, D, F) (criteria for primitiveness, Franzén, 1987). Nuclear chromatin is condensed into closely packed granules. In *Chaetoderma* the acrosome lies at the tip of a long, apical dense tube which lacks nuclear material (Fig. 25 A, C). A structure termed the "apical horn" caps the nucleus and plugs the base of the apical dense tube. The proximal centriole in *Chaetoderma* uniquely produces a flagellum, which is eliminated after apparently functioning in the elongation of the apical tube. (See Buckland-Nicks and Chia, 1989, for a full description of spermiogenesis in *Chaetoderma*.)

The spermatozoa of the neomenioid *Micromenia* are modified in several respects (Fig. 25 E). The nuclear chromatin is condensed into twisted fibers, the mid-piece has only two mitochondria and probably one centriole, the acrosome forms the apical tube, and the flagellum of the tail is wrapped by a helical process.

The primitive spermatozoa of chaetoderms suggest external fertilization. In neomenioids, modifications in spermatozoa coupled with the reproductive anatomy support the conclusion that fertilization is internal.

Larval development is either lecithotrophic or direct (summarized in Hadfield, 1979). Time from settlement to maturation of ova is one year or less in *Prochaetoderma yongei* living at depths of 2,000 m and at temperatures near 0°C (Scheltema, 1987).

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## Literature Cited

- Baba, K. (1940) The mechanisms of absorption and excretion in a Solenogastre, *Epimenia verrucosa* (Nierstrasz), studied by means of injection methods. J. Dept. Agric. Kyusyu Imp. Univ. 6: 119-166.
- Beedham, G. E. and E. R. Trueman (1968) The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. J. Zool. 154: 443-451, 2 figs.
- Buckland-Nicks, J. and F.-S. Chia (1989) Spermiogenesis in *Chaetoderma* sp. (Aplacophora). J. Exp. Zool. 252: 308-317.
- Deimel, K. (1982) Zur Ableitung des Radulaapparates der Chaetodermatidae (Mollusca, Caudofoveata). Zeit. Zool. Syst. Evol. 20: 177-187.
- Franzén, Å. (1987) Spermatogenesis. In A. C. Giese, J. S. Pearse and V. B. Pearse (eds.), Reproduction of Marine Invertebrates. IX. General Aspects: Seeking Unity in Diversity. Palo Alto, California, Blackwell Scientific Publications, and Pacific Grove, California, Boxwood Press, pp. 1-47.
- Goodrich, E. S. (1945) The study of nephridia and genital ducts since 1895. Quart. J. Microscop. Sci. 86: 115-392.
- Haas, W. (1981) Evolution of calcareous hardparts in primitive molluscs. Malacologia 21: 403-418, 14 figs.
- Hadfield, M. G. (1979) Aplacophora, In A. C. Giese and J. S. Pearse (eds.), Reproduction of marine invertebrates Vol. 5. Molluscs: Pelecypods and lesser classes. New York: Academic Press, pp. 1-25.
- Haszprunar, G. (1986) Fein morphologische Untersuchungen an Sinnesstrukturen ursprünglicher Solenogastres (Mollusca). Zool. Anz. 217: 345-362.
- Haszprunar, G. (1987) The fine morphology of the osphradial sense organs of the Mollusca. IV. Caudofoveata and Solenogastres. Phil. Trans. Roy. Soc. London B 315: 63-73.
- Heath, H. (1905) The morphology of a solenogastre. Zool. Jahrb. (Abt. Anat. Ontogenie Thiere) 21: 703-734, pl. 42-43.
- Heath, H. (1911) The solenogastres. Reports on the scientific results of the expedition to the tropical Pacific...by the "Albatross." Mem. Mus. Comp. Zool. (Harvard Univ.) 45(1): 1-179.

- Heath, H. (1912) *Spengelomenia*, a new genus of solenogastres. Zool. Jahr., Suppl. 15(1): 465-478.
- Hoffman, S. (1949) Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. Zool. Bid. Uppsala 27: 293-427.
- Pruvot, G. (1891) Sur l'organisation de quelques Néoméniens des côtes de France. Arch. Zool. Exp. Gén. (ser. 2), 9: 699-805.
- Rieger, R. M. and W. Sterrer (1975) New spicular skeletons in Turbellaria, and the occurrence of spicules in marine meiofauna. Part II. Zeit. Zool. Syst. Evol. 13: 249-278.
- Salvini-Plawen, L. v. (1967) Neue Scandinavische Aplacophora (Mollusca, Aculifera). Sarsia 27: 1-63, 63 figs.
- Salvini-Plawen, L. v. (1968a) Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). Sarsia 31: 131-142.
- Salvini-Plawen, L. v. (1968b) Über Lebendbeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. Sarsia 31: 105-126.
- Salvini-Plawen, L. v. (1970) *Phyllomenia austrina*, ein phylogenetisch bedeutsamer Solenogaster (Mollusca, Aculifera). Zeit. Zool. Syst. Evol. 8: 297-309.
- Salvini-Plawen, L. v. (1978) Antarktische und subantarktische Solenogastres (eine Monographie: 1898-1974). Zoologica (Stuttgart) 44: 1-315.
- Salvini-Plawen, L. v. (1985) Early evolution and the primitive groups. In E. R. Trueman and M. R. Clarke (eds.), The Mollusca, Vol. 10. Evolution. Orlando, Florida, Academic Press, Inc., pp. 59-150.
- Scheltema, A. H. (1972) The radular of the Chaetodermatidae (Mollusca, Aplacophora). Zeit. Morph. Tiere 72: 361-370.
- Scheltema, A. H. (1973) Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). Zeit. Morph. Tiere 76: 97-107.
- Scheltema, A. H. (1978) Position of the class Aplacophora in the phylum Mollusca. Malacologia 17: 99-109.
- Scheltema, A. H. (1981) Comparative morphology of the radulae and alimentary tracts in the Aplacophora. Malacologia 20: 361-383, 11 figs.

- Scheltema, A. H. (1985) The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca: Chaetodermomorpha). Biol. Bull. (Woods Hole) 169: 484-529.
- Scheltema, A. H. (1987) Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei*. Mar. Ecol. Prog. Ser. 37: 171-180.
- Scheltema, A. H. (1988) Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. Am. Mal. Bull. 6: 57-68.
- Scheltema, A. H., K. Kerth, and A. M. Kuzirian (In press) Aplacophora and the primitive molluscan radula. Malacologia.
- Scheltema, A. H. and A. M. Kuririan. (In press) *Helicoradomenia juani* n.g., n.sp., a Pacific hydrothermal vent aplacophoran (Mollusca, Neomeniomorpha). Veliger.
- Schwabl, M. (1955) *Rupertomenia fodiens* nov. gen. nov. sp. eine neue Lepidomeniide von der Sudwestküste Schwedens. Öst. zool. Zeit. 6: 90-146.
- Welsch, U. and V. Storch (1973) Comparative Animal Cytology and Histology. Seattle, Washington: University of Washington Press.



Table 1. Illustrated species

Species	Locality	Source*	Original publication
<u>Light microscopy, SEM</u>			
Neomeniomorpha:			
<i>Acanthomenia</i> sp.	W. European Basin, 2897 m 55°07'N, 12°53'W	CENTOB (INCAL)	herein
<i>Dorymenia</i> sp.	Iberian Basin, 681 m 36°50'N, 9°15'W	CENTOB (BALGIM)	herein
<i>Eleutheromenia</i> sp.	Bass Str. (Australia), 140 m 38°53'S, 148°25'E	VM	herein
<i>Gymnomenia</i> sp.	Namibia Basin, 620 m 23°00'S, 12°58'E	WHOI (AII-42)	herein
<i>Helicoradomenia juani</i> Schelt. + Kuzir.	Juan de Fuca Ridge, 2250 m 47°57'N, 129°06'W	NMNH	herein
<i>Lyratoherpia</i> sp.	W. European Basin, 2091 m 58°00'N, 10°40'W	CENTOB (INCAL)	herein
<i>Ocheyoherpia</i> sp.	MacQuarie Is., 11-14 m	AM	herein
New genus	W. European Basin, 2091 m 58°00'N, 10°40'W	CENTOB (INCAL)	herein
Chaetodermomorpha:			
<i>Chaetoderma nitidulum</i> <i>canadense</i> Nierstr.	St. Margaret's Bay, Nova Scotia, 74 m	Scheltema	Scheltema, 1973, 1978; herein
<i>Limifossor talpoideus</i> Heath	Southern Alaska, ~540 m	Scheltema	Heath, 1905; herein

Table 1 (continued)

Species	Locality	Source*	Original publication
<u>TEM, SEM</u>			
Neomeniomorpha			
<i>Aesthoherpia glandulosa</i> Salv.-Pl.	off Blomsterdalen, Norway	Haszprunar	Haszprunar, 1986
<i>Micromenia fodiens</i> (Schwabl)	off Blomsterdalen, Norway	Wolter	herein
<i>Neomenia carinata</i> Tullberg	off Banyuls-sur-Mer, France	Haszprunar	Haszprunar, 1987; herein
Chaetodermomorpha			
<i>Chaetoderma argenteum</i> Heath	off Bamfield, British Columbia	Buckland-Nicks	Buckland-Nicks and Chia, 1989; herein
<i>Chaetoderma nitidulum</i> Lovén	off Blomsterdalen, Norway	Tscherkassky	herein
<i>Falcidens crossotus</i> Salv.-Pl.	off Blomsterdalen, Norway	Tscherkassky	herein
<i>Scutopus ventrolineatus</i> Salv.-Pl.	off Blomsterdalen, Norway	Tscherkassky	herein
<i>Scutopus robustus</i> Salv.-Pl.	off Blomsterdalen, Norway Bay of Biscay	Tscherkassky CENTOB (THALASSA)	herein herein

\*CENTOB = Centre National de Tri d'Océanographie Biologique, IFREMER, Brest, France

VM = Museum of Victoria, Melbourne, Victoria, Australia

WHOI = Woods Hole Oceanographic Institution, Woods Hole, MA

NMNH = National Museum of Natural History, Washington, DC

AM = Australian Museum, Sydney, New South Wales, Australia

Cruise names in parentheses.

See Acknowledgments for personal names other than authors.



## ILLUSTRATIONS

Figure 1. Anatomy of generalized neomenioid Aplacophora. A: Anterior. B: Posterior. C: Nervous system (after Schwabl, 1955). BU, buccal commissure leading to 2 pairs of buccal ganglia; C, cuticle; CG, cerebral ganglion; CM, circular muscles; CPM, circumpharyngeal muscle; CS, copulatory spicule, pocket indicated by dashed lines; DC, dorsal cecum; DS, dorsal sinus/aorta; DSO, dorsoterminal sense organ; DSP, dorsofrontal sensory pit; EP, epidermal papilla; ES, esophagus; F, foot; G, gonad; GD<sub>1,2</sub>, upper, lower gametoduct; GP, gametopore; GPC, gonopericardial duct; HC, hemocoel; LM, longitudinal muscles; LN, lateral nerve cord; MB, membranoblast; MC, mantle cavity; MG, midgut; MO, mouth opening; OB, odontoblast; OC, oral cavity; OD, odontophore; OM, oblique muscles; OV, ovum; P, pedal pit; PC, pericardial cavity; PCG, precerebral ganglion/nerve; PG, pedal gland; PH, pharynx; R, radula; RB, radula bolster; RE, rectum; RP, respiratory papilla; SC, suprarectal commissure; SE, superior epithelium; SG, salivary gland/cell; SP, spicule, spicule hole; SR, seminal receptacle; SV, seminal vesicle; V, ventricle; VE, vestibule; VLM, ventral longitudinal muscle; VN, ventral nerve cord; VP, ventral radular pocket; VSG, ventral salivary gland.

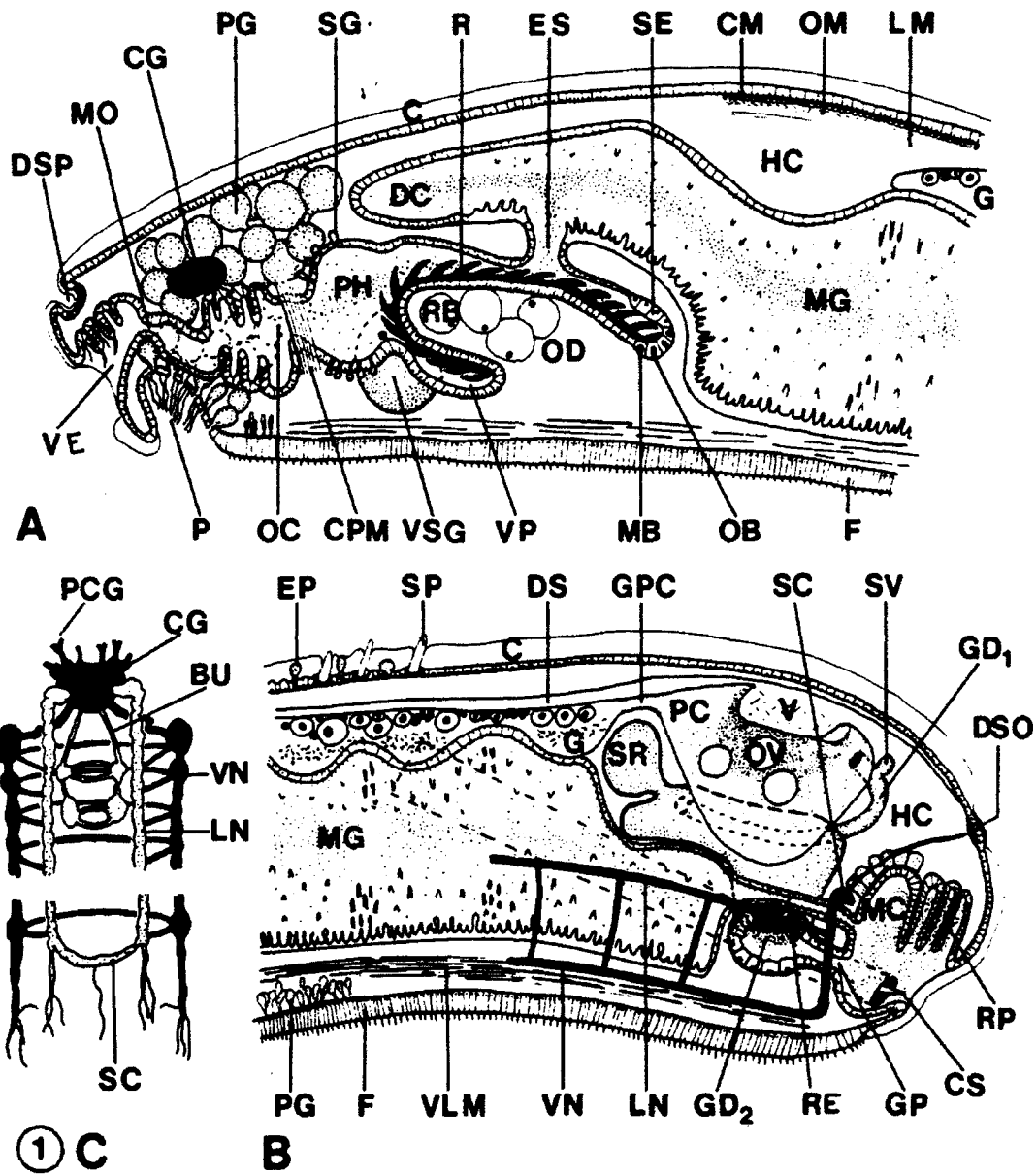


Figure 2. Anatomy of chaetoderm Aplacophora *Limifossor talpoides* Heath. A: Anterior. B: Posterior. (After Heath, 1905.) Abbreviations as in Figure 1 except B, blood lacuna; CT, ctenidium; DG, digestive gland; I, intestine; OS, oral shield; S, septum (dorsally as dashed lines); ST, stomach.

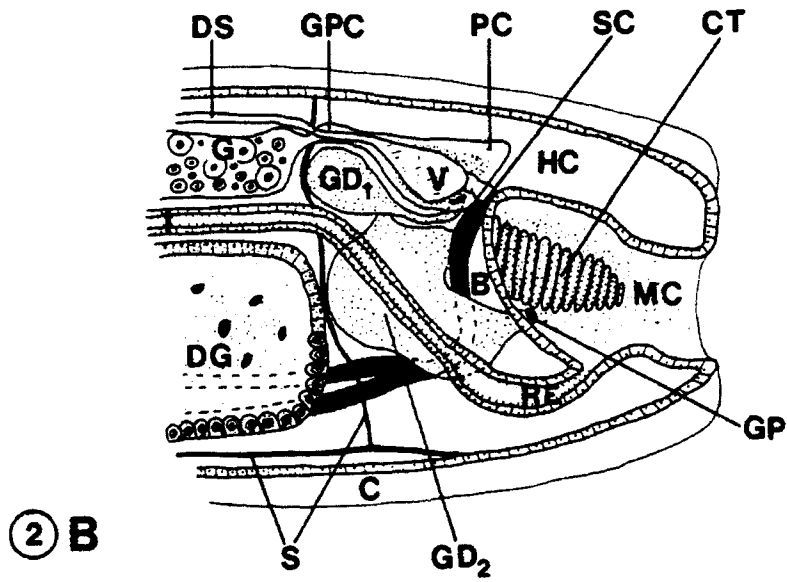
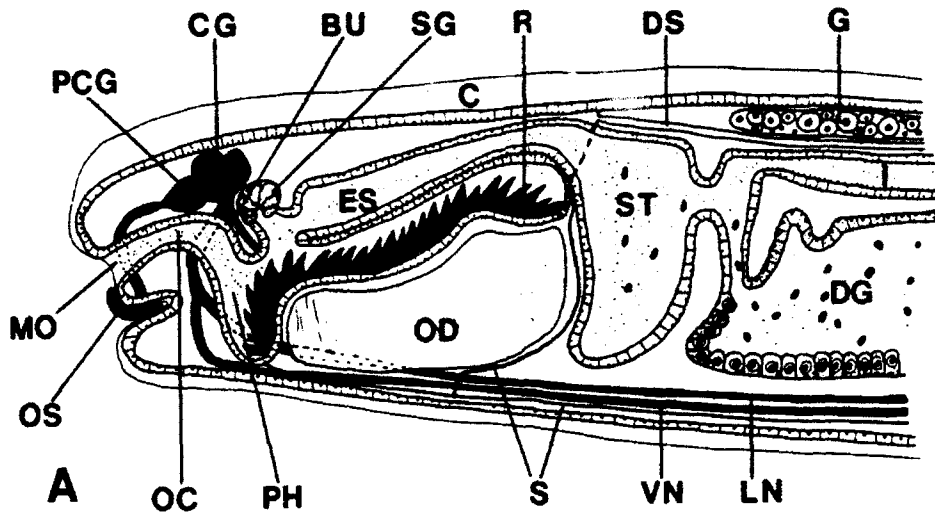


Figure 3. External anatomy of Neomeniomorpha. A, C: *Eleutheromenia* sp. (anterior toward right), squat species with erect, hollow spicules, many fish-hook shaped; hollow core of broken spicules hexagonal (arrowheads). B, D: *Lyratoherpia* sp. (anterior toward left), elongate, smooth species with two types of solid, flat spicules; ventral posterior bulge (asterisk) due to large copulatory spicule gland (cf. Figs. 23A, 24H). F, foot; MC, mantle cavity opening; MO, mouth opening. Scale bars: A, B = 0.5 mm, C, D = 20  $\mu$ m.

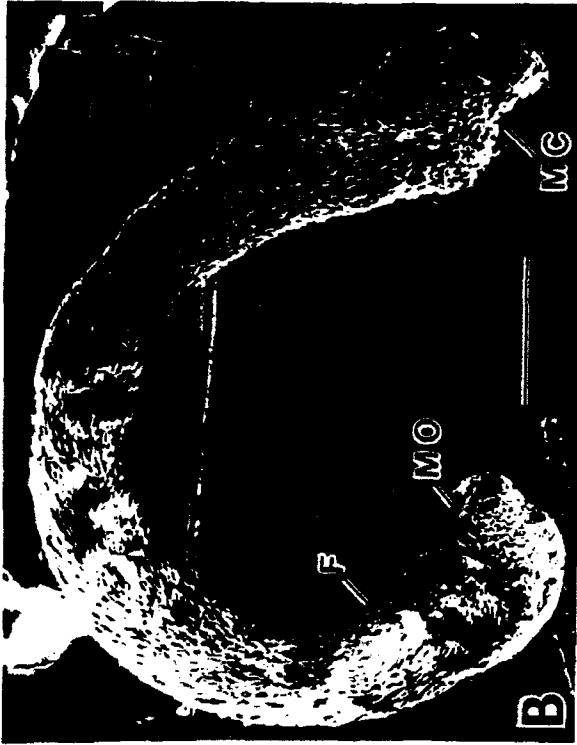


Figure 4. External anatomy of Chaetodermomorpha. A, B: Living specimens of *Chaetoderma nitidulum canadense*; principal characters include oral shield (arrowheads), anterior constriction (arrow), body region 1 containing digestive gland, gonad, and intestine, and body region 2 containing stomach and heavy longitudinal muscle bands. (Photos R. Robertson.) C: Ctenidia of *Chaetoderma argenteum* extended from mantle cavity showing gill-folds and efferent channels. (Photo J. Buckland-Nicks.) D: Spicules from body region 1, *C. n. canadense*. MC, mantle cavity. Scale bars: A = 10 mm, B = 5 mm, C = 200  $\mu\text{m}$ , D = 100  $\mu\text{m}$ .



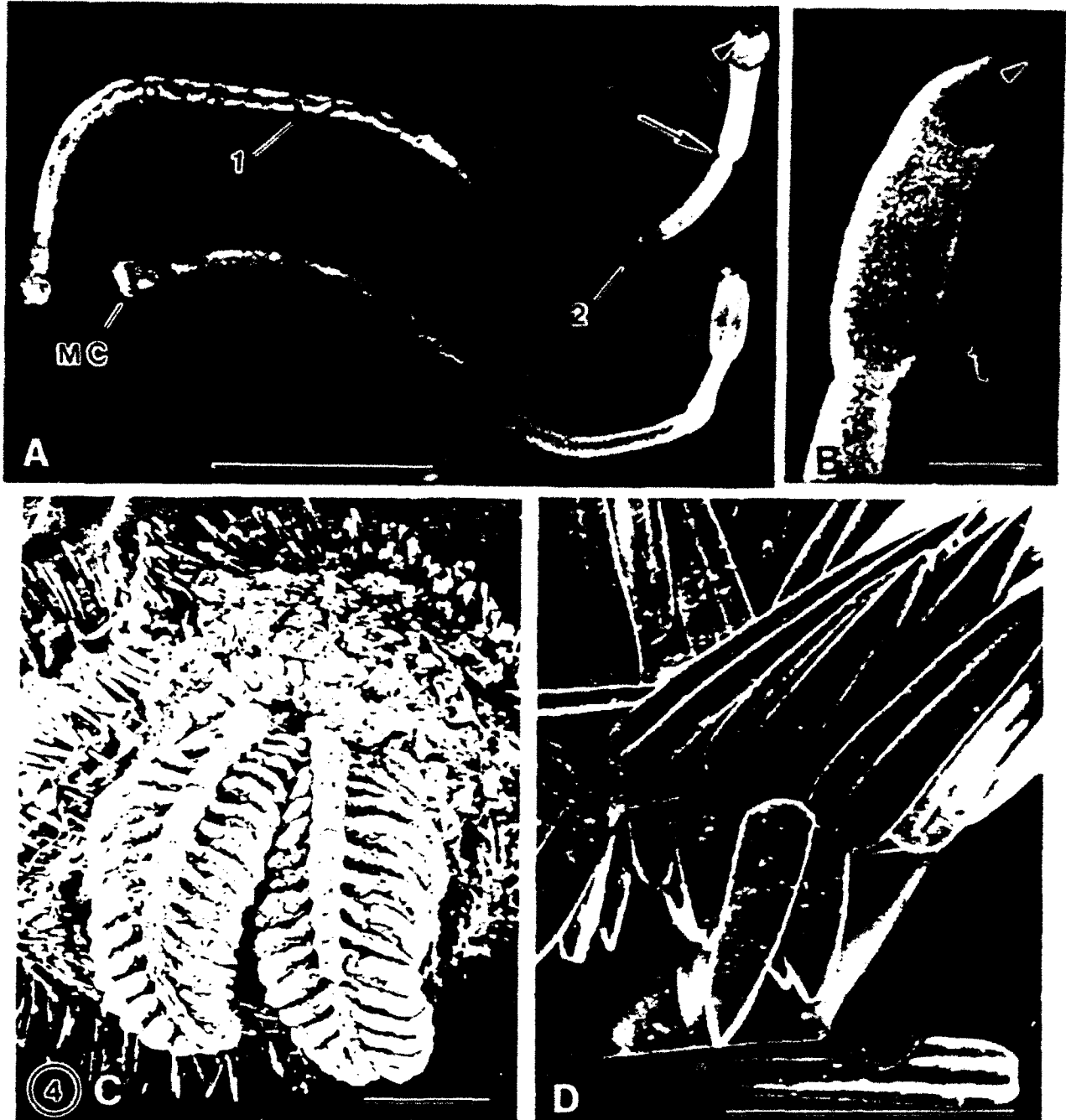


Figure 5. Epidermis and cuticle. A: Multicellular epidermal papilla, *Neomenia carinata*; epidermis underlain by thick dermis; fibers from epidermis to cuticle (arrowhead) indicate cuticle secretion. (From Haszprunar, 1987.) B: Channel through body-wall musculature between hemocoel and epidermis, *Helicoradomenia juani*; blood cells indicated by arrowheads. C: Stalked epidermal papilla (arrow) in thick cuticle of *Dorymenia* sp., epidermis relatively thin; depressions in cuticle (arrow) remain after papillae discharge contents to outside; body-wall musculature underlies epidermis; voids indicate dissolved skeletal spicules (asterisks) arranged at right angles to each other. D: Nerve fibers (arrowheads) and E: Muscle fibers (arrow) passing through body-wall musculature to epidermis, *H. juani*. F: Thick epidermis relative to cuticle with dissolved spicule voids, *Acanthomenia* sp. G: Thin epidermis and very thin cuticle without obvious spicule voids, *Lyratoherpia* sp. (cf. Fig. 3 B, D). Note diversity of unstalked epidermal gland cells in B, D-G. C, cuticle; DE, dermis; E, epidermis; EP, epidermal papilla; HC, hemocoel; MU, muscle layer; SP, spicule hole. Scale bars: A = 5  $\mu\text{m}$ , B = 10  $\mu\text{m}$ , C = 100  $\mu\text{m}$ , D, F, G = 20  $\mu\text{m}$ , E = 50  $\mu\text{m}$ .



Figure 6. Epidermis and body-wall musculature. A: Sagittal section, ventral portion of body, *Scutopus ventrolineatus*; from top, lower gametoduct with infolded epithelium, ventral nerve cord with perikarya of ganglion, longitudinal muscles, circular muscles, epidermis and cuticle. B: Unstalked, two-celled epidermal papilla, *Falcidens crossonius*; distal cell with blood-cell characteristics and membrane-bound vesicles (arrow) (cf. Fig. 14 D); thick matrix of connective tissue between muscles (cf. Fig. 13 G); fibers from epidermis (arrowheads) indicate cuticle secretion; cuticle fibers parallel to epidermis. C: Cuticle with parallel fibers and thick connective tissue matrix between muscle fibers, *Chaetoderma nitidulum*. D: Spicule formation, *S. ventrolineatus*, spicule removed by decalcification, base only shown; microvilli underlie base of organic cap of calcium-carbonate-secreting cell (1), myoneme fibers (arrow) putatively contribute to mobility of spicule; neighboring cells (2) seal off crystallization chamber by tight junctions (arrowheads). E: Multiciliated and glandular epidermis of foot, *Micromenia fodiens*, sagittal section. (Photo K. Wolter.) C, cuticle; CM, circular muscles; E, epidermis; EP, epidermal papilla; GC, gland cell; GD<sub>2</sub>, lower gametoduct; LM, longitudinal muscles; MV, microvilli; N, nucleus; SP, spicule hole; VN, ventral nerve cord. Scale bars: A, C-E = 10  $\mu$ m, B = 5  $\mu$ m.

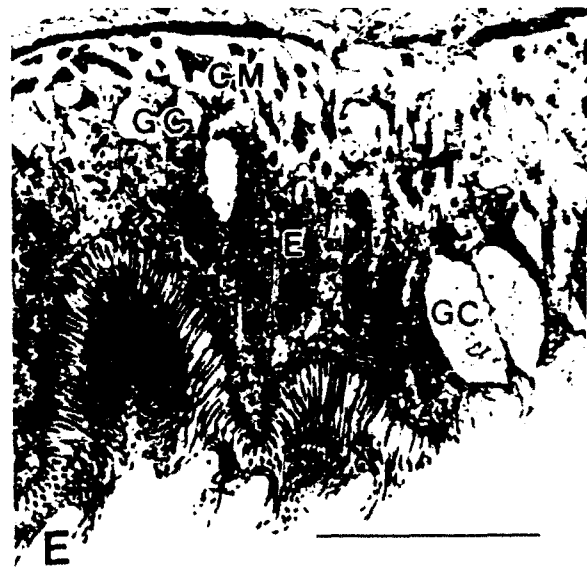
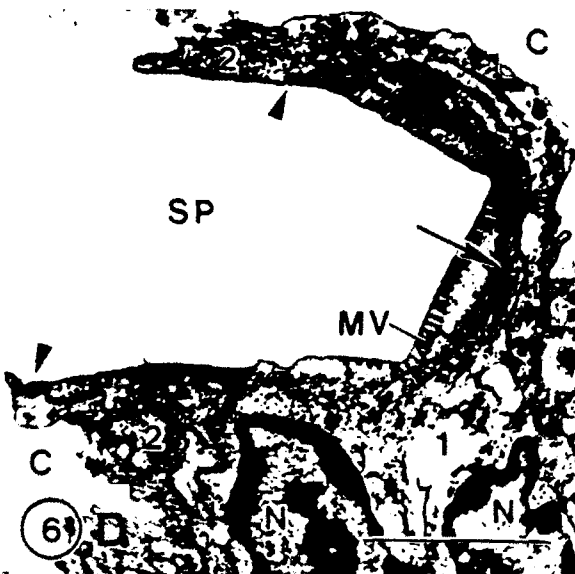
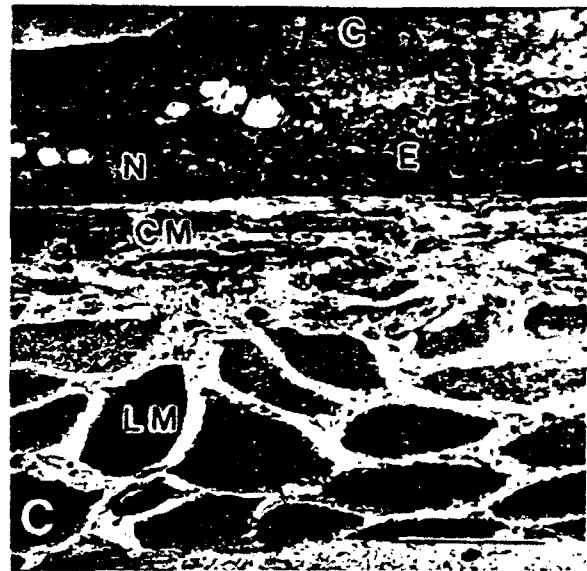
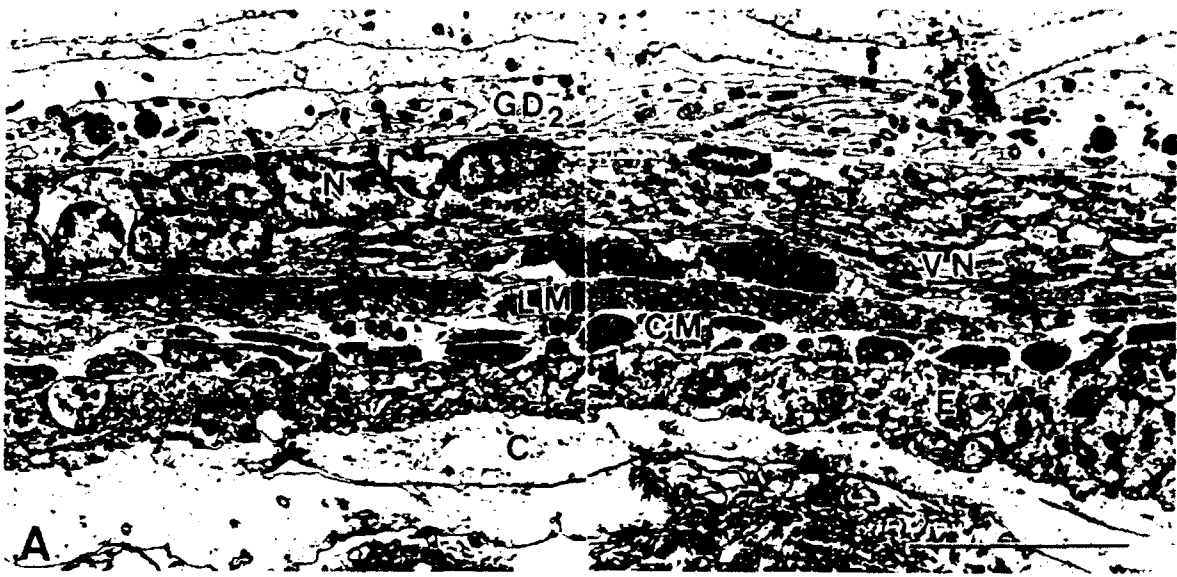


Figure 7. Neomenioid vestibule. A: Dense cirri between mouth and proximal end of vestibule with many short glandular papillae (asterisk), *Eleutheromenia* sp.; vestibule appears ventral owing to plane of section. B: Long, slender vestibular papillae, *Dorymenia* sp., illustrating central muscle fibers (arrows) and underlying nerve net with nerve fibers extending to center of papillae; arrowheads indicate several ganglia; papillae truncated by sectioning. C: Cross-section through distal end of single vestibular papilla, *Aesthoherpia glandulosa*; cortical cell (2) with a centrally situated nucleus envelops sensory cilia and basal bodies (arrow) and lies within more lucent peripheral cells (1). (From Haszprunar, 1986.) MO, mouth opening; MV, microvilli; N, nucleus; VE, vestibule. Scale bars: A, B = 50  $\mu\text{m}$ ; C = 2  $\mu\text{m}$ .

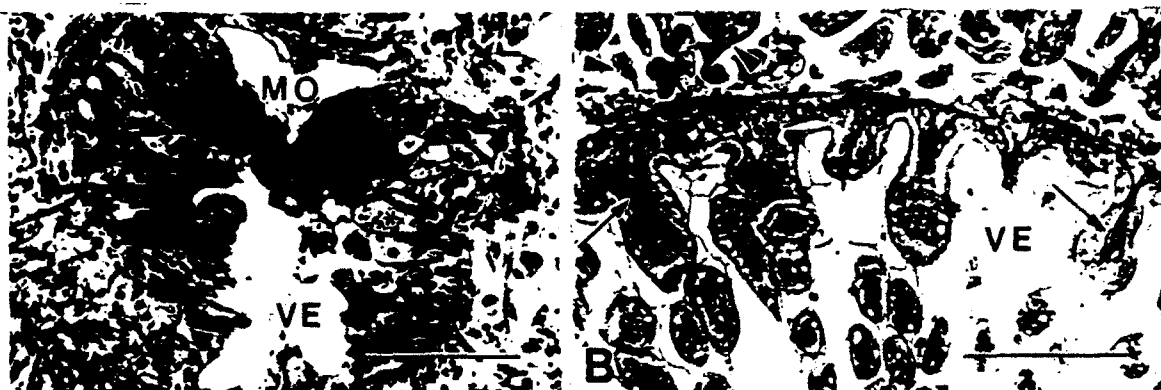


Figure 8. Neomenioid vestibule and oral cavity. A: Vestibule with few squat papillae, *Ocheoherpia* sp.; large dorsal sinus lies above. B: Sensory cirrus (arrowhead) and glandular epithelium of vestibular papillae, *Helicoradomenia juani*; epithelium above vestibule is beginning of oral cavity wall. C: Oral cavity with folds, *Ocheoherpia* sp.; dorsal sinus, paired dorsal ceca of midgut, and cerebral ganglion are dorsal; dorsal and lateral are large, compound pedal glands that open ventrally into pedal pit (arrowhead). D: Folded oral cavity epidermis with sensory cirrus (arrowhead) and dorsal salivary gland, *H. juani*. CG, cerebral ganglion; DC, dorsal cecum; DS, dorsal sinus; OC, oral cavity; P, pedal pit; PG, pedal gland; SG, salivary gland; VE, vestibule. Scale bars: A, C = 100  $\mu\text{m}$ , B, D = 50  $\mu\text{m}$ .





8

Figure 9. Chaetoderm oral shield. A: External view of oral shield with peripheral gland openings (arrowheads) and dorsal cleft (arrow), *Falcidens crossotus*. B: Transition between cuticular oral shield (1) and body cuticle (2), *F. crossotus*; matrix morphologically similar, oral shield with dumbbell-shaped granules in dense outer layer (arrowheads) and interdigitated microvilli. C: Peripheral gland cells penetrating cuticular oral shield, *Scutopus ventrolineatus*; mucus contained in large vacuoles separated by limiting plasma membranes. D: Mouth opening, *F. crossotus*; oral shield epithelium, lower right, with gland cell; oral cavity epithelium (arrowheads) distinct with numerous vacuoles containing dark granules; dumbbell-shaped granules continue as scattered bodies in oral cavity cuticle. E: Sensory cilium (arrow) of oral shield, *F. crossotus*; cell boundary indicated by arrowheads, adjacent to nerve (right). F: Sensory cell with cilium (arrows) penetrating cuticular oral shield, *F. crossotus*; dense layer (arrowheads) as in B. C, cuticle; GC, gland cell; MO, mouth opening; MV, microvilli; SI, sensory cell; SP, spicules. Scale bars: A = 100  $\mu\text{m}$ , B, D = 10  $\mu\text{m}$ , C, F = 5  $\mu\text{m}$ , E = 1  $\mu\text{m}$ .

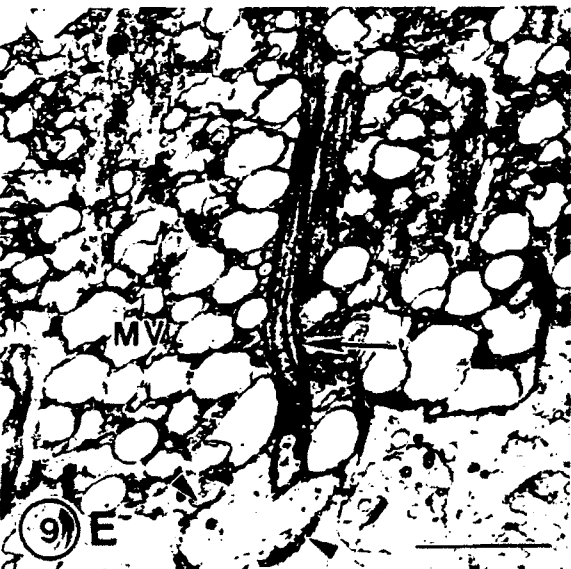
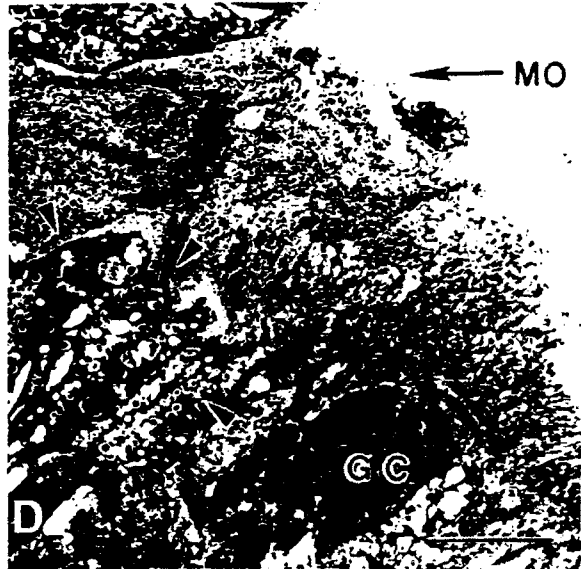
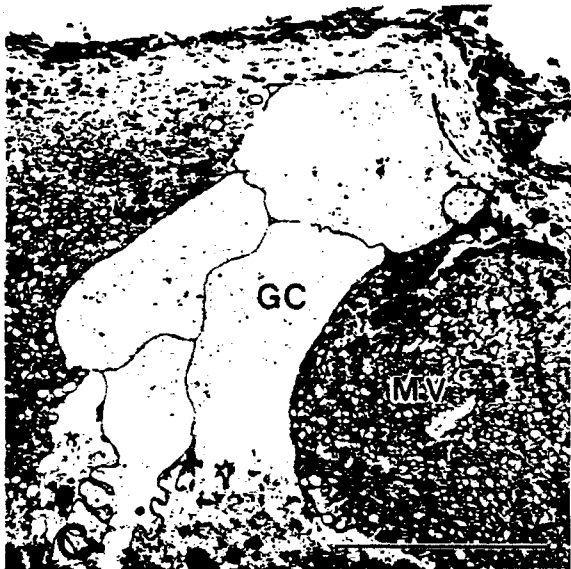
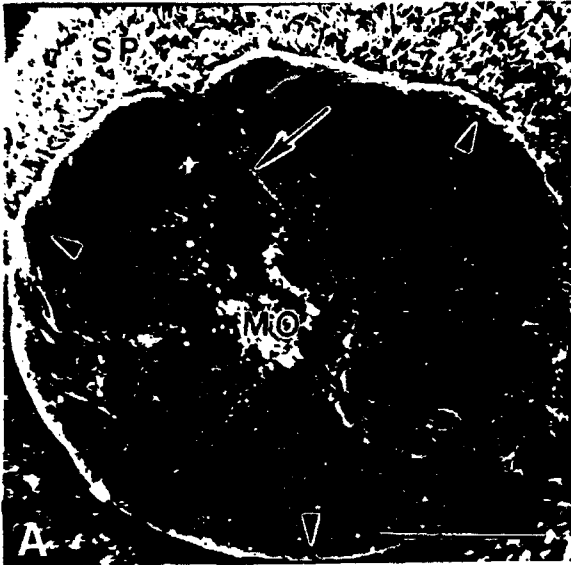


Figure 10. Neomenioid anterior sensory structures, pedal pit, and foot. A: Dorsofrontal sensory pit lined by cuticle, sagittal section, *Helicoradomenia juani*; sensory cells indicated by arrowhead. B: Pedal pit, *H. juani*, with pedal glands discharging into it; undischarged gland cells (arrowhead) stained dark. C: Foot, *Dorymenia* sp., with blood lacuna (asterisk) from hemocoel within foot-fold; foot epithelium heavily ciliated (cf. Fig. 6 E); lateral wall of foot groove bears spiculeless cuticle (arrowheads); gland cells indicated by arrow. D: Foot of *H. juani*, symbols as in C. E: Compound pedal gland cells, *H. juani*, with branched ducts, F, G: Cirrus anterolateral to ciliated pedal pit, *Aesthoherpia glandulosa*; cell 1 same in each photo; cirrus occupies deep pocket (arrowheads) adjacent to muscles and surrounded by nerve tissue. (From Haszprunar, 1986.) C, cuticle; MU, muscles; P, pedal pit; PG, pedal gland. Scale bars: A, E = 20  $\mu\text{m}$ , B, C = 50  $\mu\text{m}$ , D = 40  $\mu\text{m}$ , F, G = 5  $\mu\text{m}$ .

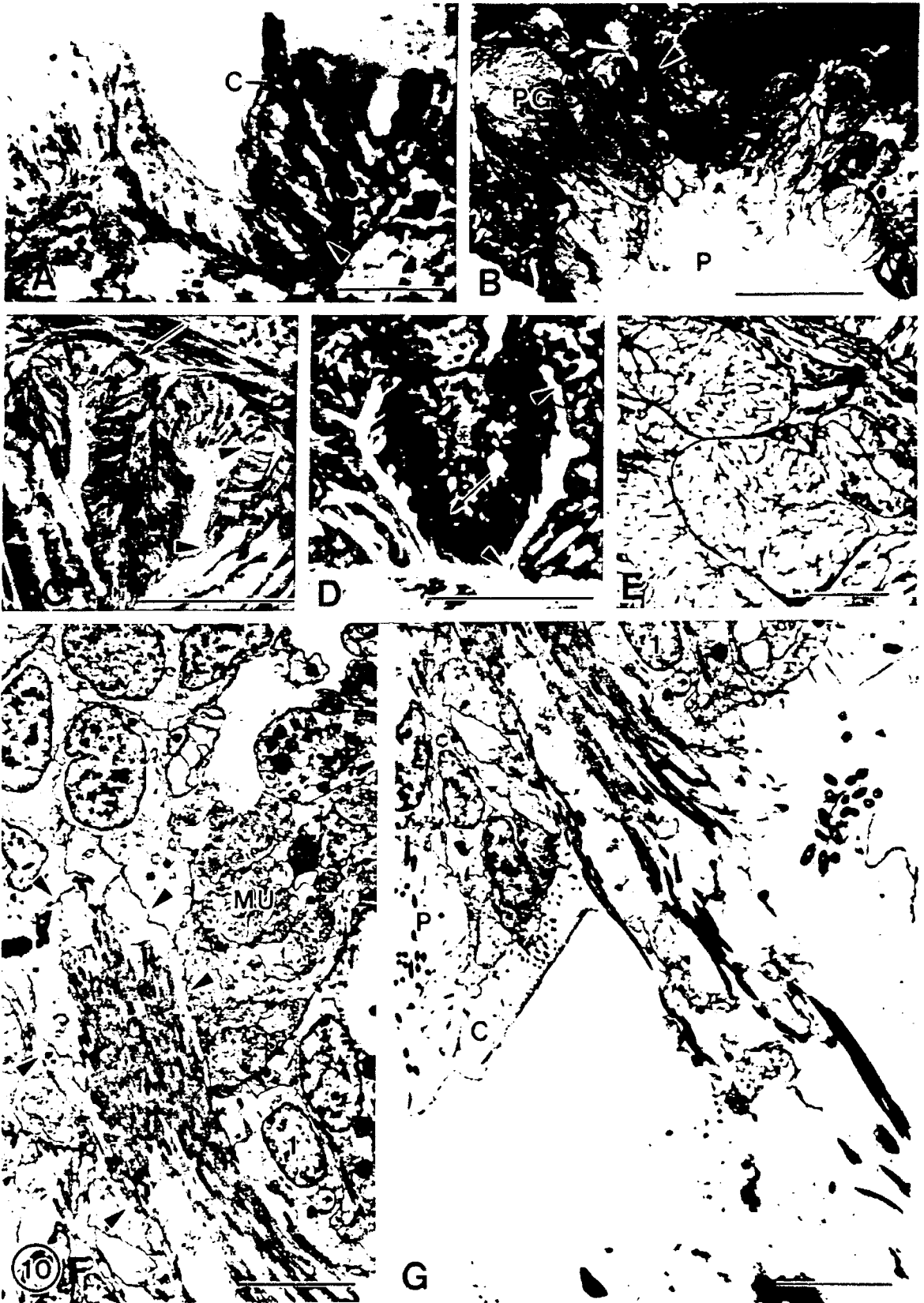


Figure 11. Mantle cavity. A, B: Frontal and cross-sections of ctenidia, *Chaetoderma nitidulum canadense* (cf. Figs. 4C, 12A, B); efferent channels, asterisks; in B, male gametopore (arrowhead); dorsal and ventral gill retractors at tips and bases of ctenidia, lateral retractors not in section. C: Low respiratory folds (arrowhead and inset), *Dorymenia* sp.; infolded cuticle-bearing mantle epithelium forms lower chamber, voids in cuticle left by dissolved accessory copulatory spicules (cf. Fig. 24 E); dorsal blood sinus and lateral blood lacunae indicated by asterisks; rotifer (arrow) lies unattached in mantle cavity, a symbiosis not previously known. D: Long respiratory papillae, *Helicoradomenia juani*; see F below. E: Epithelium with brush border, *Neomenia carinata* (see also Fig. 12C); bacteria in brush border (arrowheads) can be engulfed by epithelial cells (arrow). (Photo G. Haszprunar.) F: Distal tips of three respiratory papillae, *Helicoradomenia juani*, with cirri, gland cells, and large blood-filled lacunae from hemocoel. B, blood lacuna; C, cuticle; MC, mantle cavity; MU, muscles of gill retractor. Scale bars: A-D = 200  $\mu\text{m}$ , E = 2  $\mu\text{m}$ , F = 20  $\mu\text{m}$ .

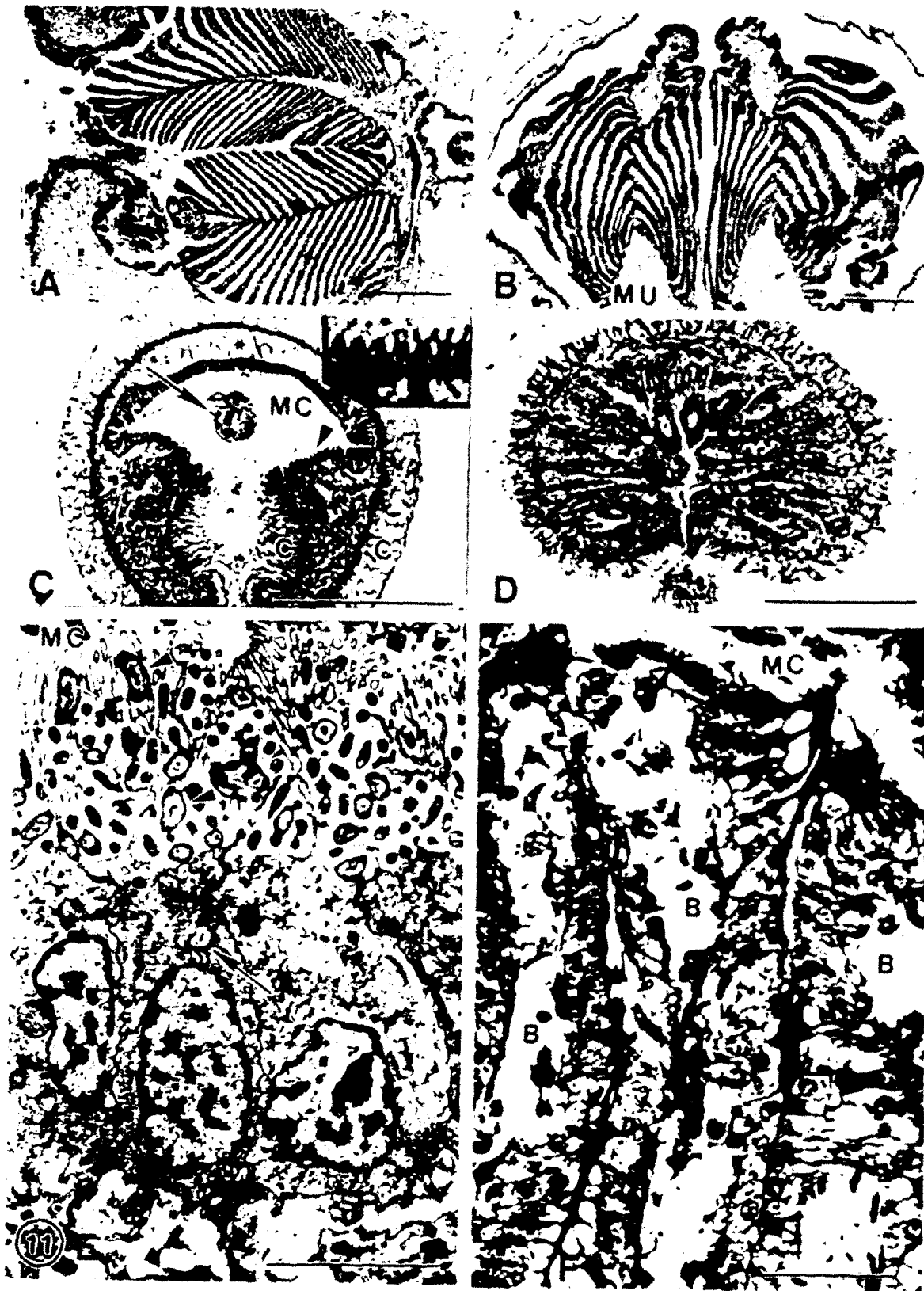


Figure 12. Chaetoderm mantle cavity. A: Gill lamella, longitudinal section of mid-portion, *Scutopus ventrolineatus*, with numerous apical mitochondria (arrowheads) indicating active transport; epithelial cells ciliated and with large nuclei and lipid droplets (asterisk); blood lacuna runs between epithelial walls. B: Gill lamella, longitudinal section of tip, *Falcidens crossotus*, with abundant lucent gland cells; epithelium with fewer cilia than A; dark lamellar bands between microvilli (arrowheads) resemble arthropod procuticle for filtering and protection. C: Mantle cavity epithelium, *S. ventrolineatus*, with abundant gland cells alternating with interstitial ciliated cells; gland cells contain amorphous vesicles with dark borders and multivesicular bodies (arrowheads); nuclei basal, underlain by Golgi complexes (arrow). D: Dorsoterminal glands of two types in mantle cavity wall, *S. ventrolineatus*, the more lucent cells with cilia; arrow indicates mitochondrion. B, blood lacuna; GC, gland cell; MC, mantle cavity; N, nucleus. Scale bars: A = 5  $\mu\text{m}$ , B-D = 10  $\mu\text{m}$ .



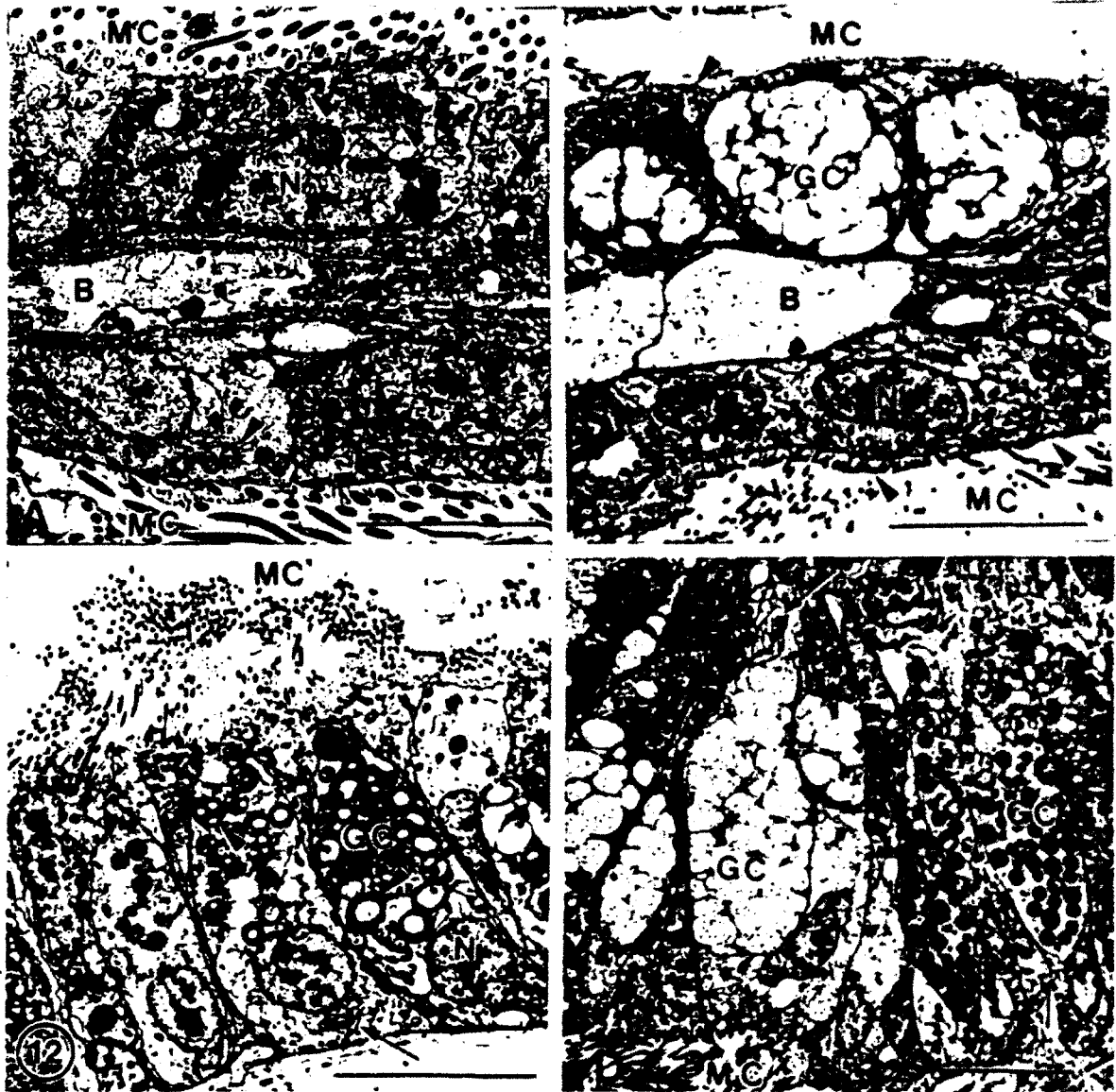


Figure 13. Muscles, nerves, and blood. A: Radular retractor muscles (6), *Dorymenia* sp., with outer connective tissue (arrowheads). B: Cross-section showing body-wall muscle layers (1, outer circular; 2, middle orthogonal oblique; 3, inner longitudinal); ventral longitudinal muscle band, 4; lateroventral muscle band, 5; and radular muscles, 6, *Dorymenia* sp.; the lateroventral band interrupts the midgut laterally (large arrow, above), attaches to foot-groove epithelium ventrally (small arrow), and connects to septum defining ventral sinus (arrowhead). C: Serially repeated lateroventral muscles (5) and midgut sacculations, sagittal section, *Gymnomenia* sp.; gonad with developing oocytes and spermatocytes (arrowhead) (cf. Fig. 23 H). D: Lateral nerve cord and commissure, *Dorymenia* sp.; body-wall muscle layers as in B. E: Blood cells (arrowheads) in hemocoel and within body-wall muscles near base of epidermal papilla (arrow), *Dorymenia* sp. F: Blood cells, *Dorymenia* sp. G: Ventral sinus and body-wall musculature (1, outer circular; 3, inner longitudinal), *Chaetoderma nitidulum canadense*; septum defining ventral sinus, arrowhead; lateral and ventral nerve cords adjacent to each other, nuclei peripheral. C, cuticle; E, epidermis; F, foot; G, gonad; HC, hemocoel; LN, lateral nerve cord; MG, midgut; MU, muscles of body wall; PG, pedal gland; ST, stomach; VN, ventral nerve cord; VP, ventral radular pocket; VS, ventral sinus; VSG, ventral salivary gland. Scale bars: A = 50  $\mu\text{m}$ , B-D, G = 100  $\mu\text{m}$ , E = 10  $\mu\text{m}$ , F = 20  $\mu\text{m}$ .

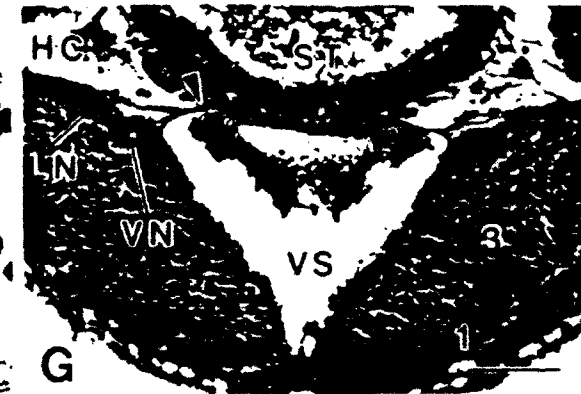
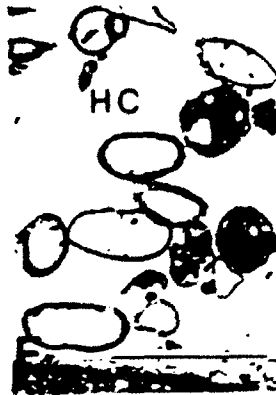
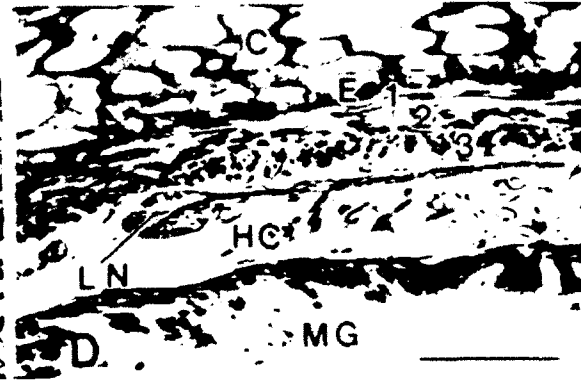
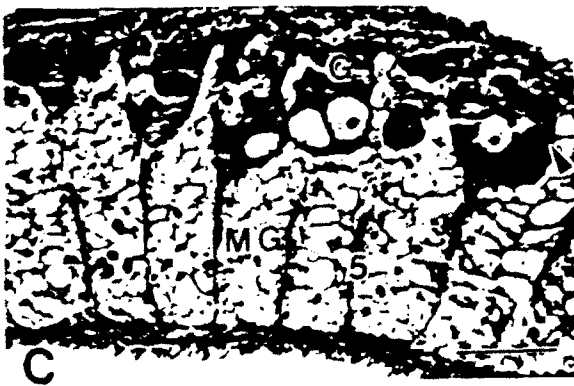
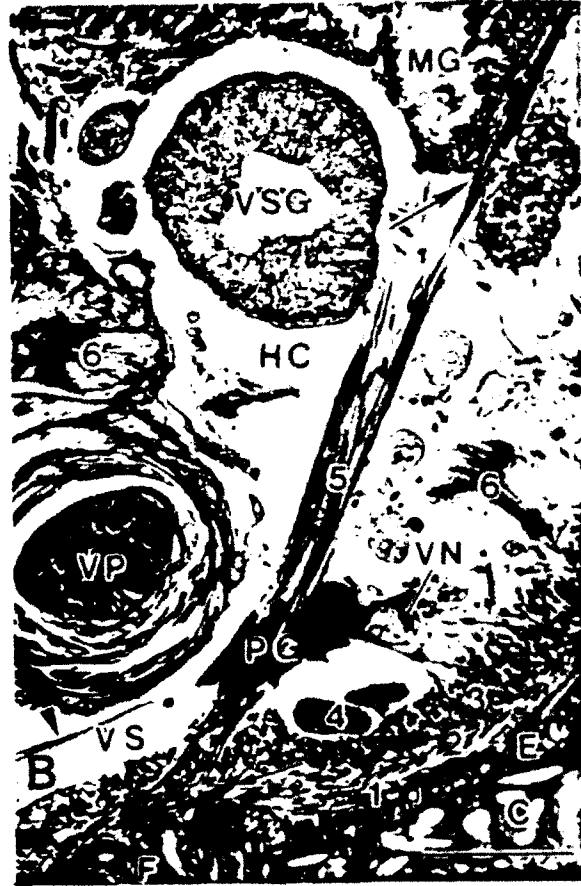
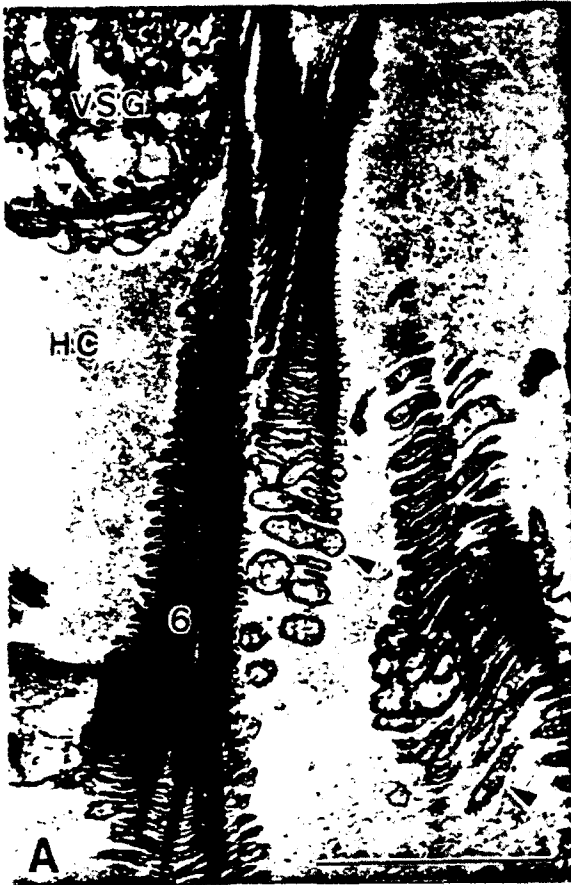


Figure 14. Chaetoderm ventricle and blood, *Scutopus ventrolineatus*. A: Section through suspensory membrane (arrows) between body wall (above) and ventricle epithelium (below), membrane continuous with membrane lining pericardial cavity; transport epithelium of ventricle wall with abundant mitochondria, infoldings (arrowhead), and muscle cells; pericardial cavity with many spermatozoa (asterisks). B: Strongly infolded ventricle cell membranes and mitochondria (arrowheads); two blood cells within lumen contain electron lucent and membrane-bound vesicles (see D). C: Ventricle wall with lumen, lower left, less contracted than B, with proximal muscles, mitochondria (arrowheads), and glycogen particles. D: Blood cell with vesicular bodies (arrowheads), rough endoplasmic reticulum (double arrowhead), and lipid droplets (asterisk). B, blood lacuna; BC, blood cell; LM, longitudinal muscle; MI, mitochondria; MU, muscle fibers; N, nucleus; PC, pericardial cavity. Scale bars: A = 10  $\mu\text{m}$ , B, C = 5  $\mu\text{m}$ , D = 1  $\mu\text{m}$ .

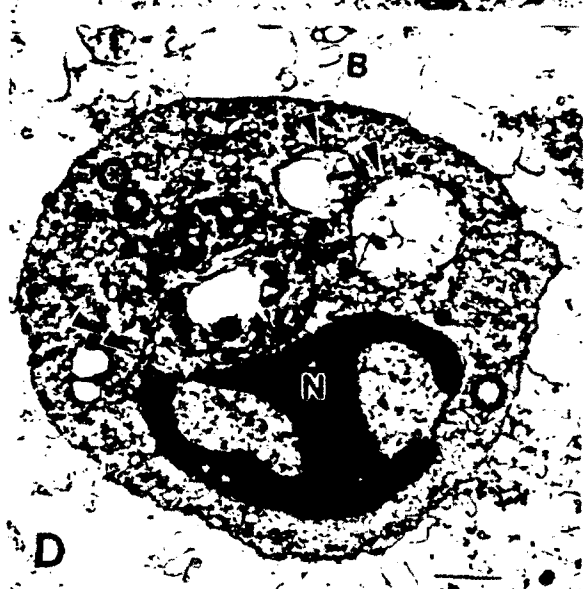
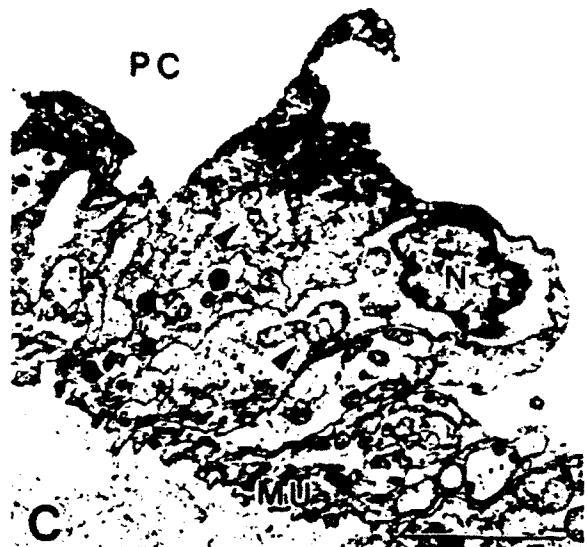
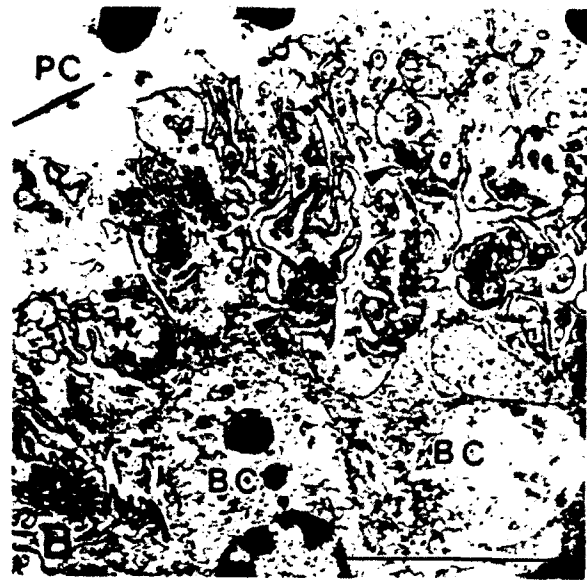


Figure 15. Nerves and dorsoterminal sense organ. A: Cerebral ganglion, *Chaetoderma nitidulum*, surrounded by glial tissue sheath, with peripheral nuclei and central neuropile. B: Ventral nerve cord beneath lower gametoduct, *Scutopus ventrolineatus*, with peripheral nuclei and axons in central neuropile, some containing neurosecretory and transmitter vesicles. C: Ganglion, *Micromenia fodiens*, with peripheral nuclei (asterisks), central axons, and thick connective tissue capsule (arrowheads). (Photo K. Wolter.) D: Dorsoterminal sense organ, *Falcidens crossotus*, with deep cleft lined by cuticle without spicules; multiciliated sensory cell without cuticle lies at base; mucous layer (asterisks) covers cuticle; thick basal lamina (arrowheads) and muscles underlie organ. Note parallel laminae of sensory cell on left. E: Dorsoterminal sense organ, longitudinal section, *Chaetoderma nitidulum*, with collar receptor protruding between microvilli of brush border; a long cilium (small arrows) extends beyond ring of microvilli (large arrow); nerve fibers extend from base of receptor; cell border indicated by arrowheads, dense vesicle by asterisk. AX, axones; C, cuticle; GD<sub>2</sub>, lower gametoduct; LM, longitudinal muscle; MI, mitochondria; N, nucleus; NF, nerve fibers; SI, sensory cell. Scale bars: A-D = 10  $\mu\text{m}$ , E = 1  $\mu\text{m}$ .

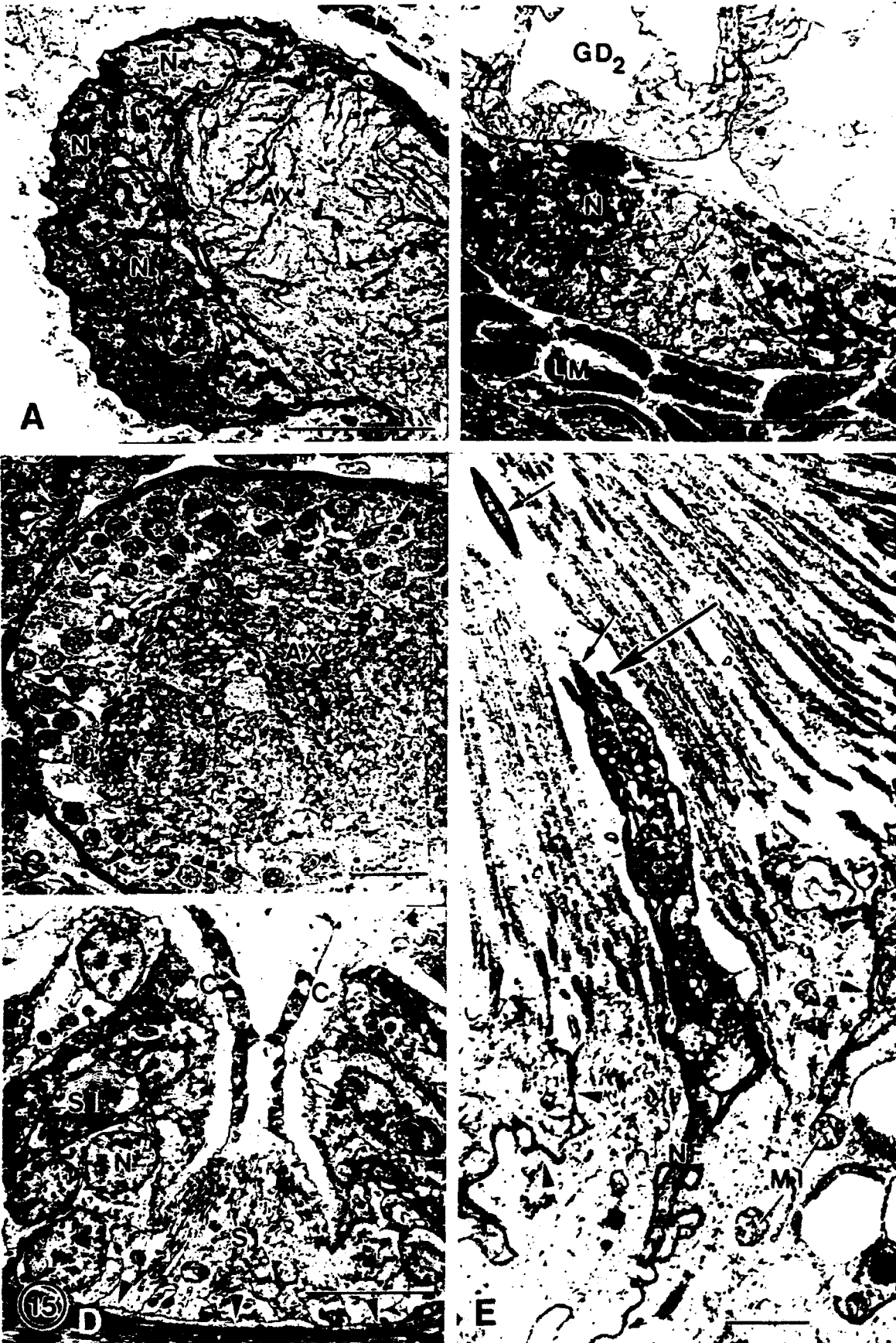


Figure 16. Neomenioid sensory organs. A: Dorsoterminal sense organ, *Neomenia carinata*, with microvilli in mucus-filled cleft (large arrow) and cilia (arrowhead) from two sensory cells showing ciliary basal bodies and rootlets (small arrow). (From Haszprunar, 1987.) B: Oral cavity, *Aesthoherpia glandulosa*, with sensory cirri (arrowheads) (cf. Fig. 8 B), sensory cells, and salivary gland cells. C: Pedal commissure sac with inclusion bodies, *Eleutheromenia* sp., lined by thick basal lamina (arrowheads) connected to septum of ventral sinus. D: Bell-shaped receptor of foot, *A. glandulosa*, with central cilium (arrowhead); foot cilia at bottom. E: Pedal commissure sac, *A. glandulosa*, lined by basal lamina (arrowheads) connected to lamina (double arrowheads) of muscular septum innervated at arrow; cells of sac have empty appearance. (B, D, E from Haszprunar, 1986.) AX, axone; F, foot; GC, gland cell; N, nucleus; PG, pedal gland; PS, pedal commissure sac; S, septum; SI, sensory cell. Scale bars: A = 2  $\mu\text{m}$ , B, E = 5  $\mu\text{m}$ , C = 50  $\mu\text{m}$ , D = 1  $\mu\text{m}$ .



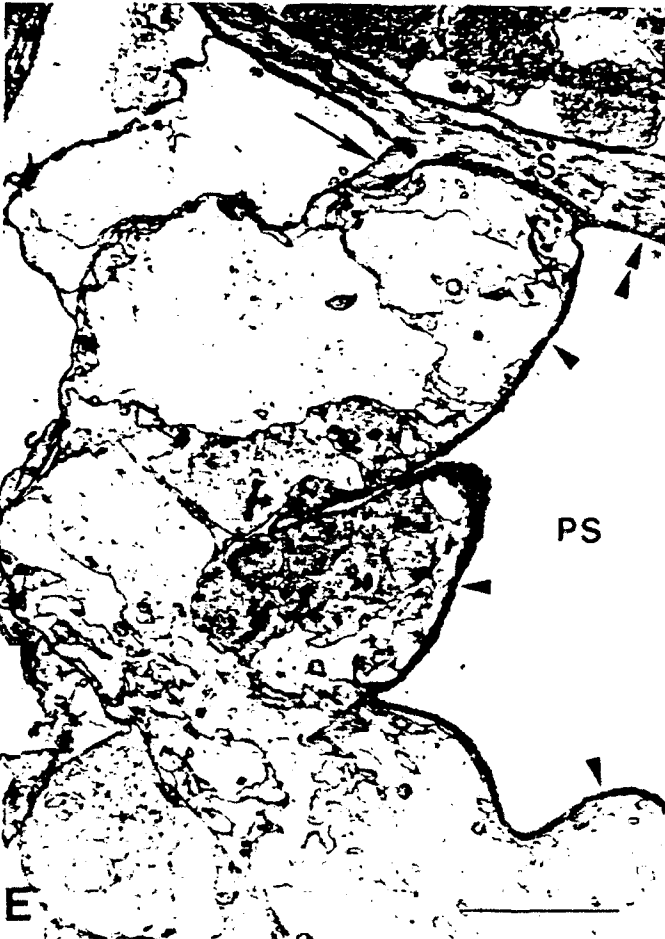
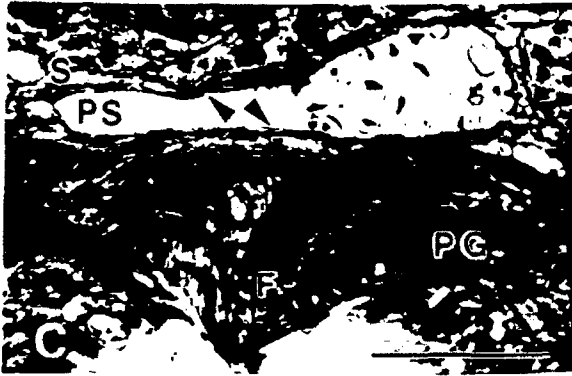
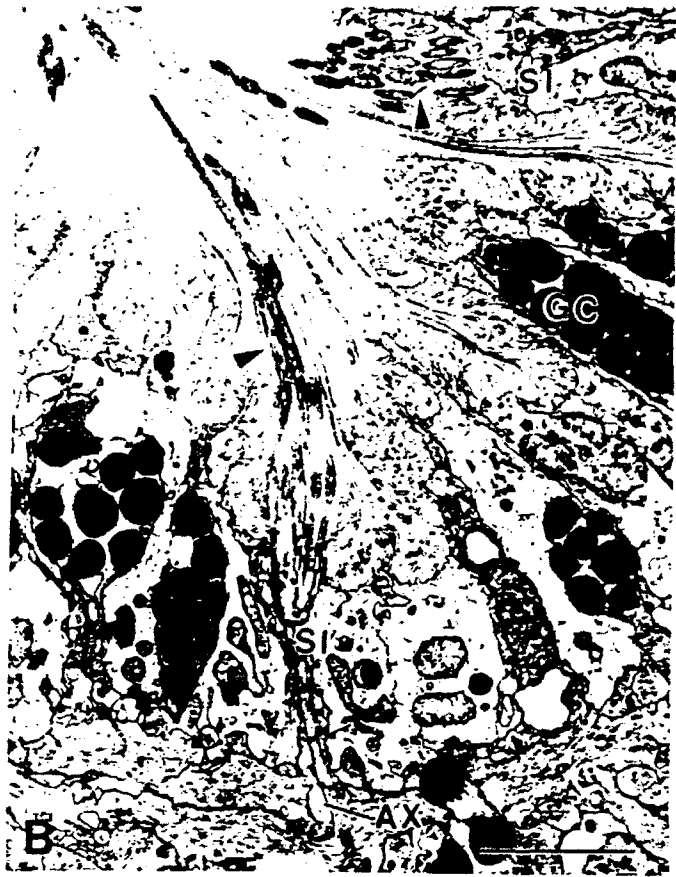


Figure 17. Digestive system. A: Oral cavity and pharynx, *Helicoradomenia juani*; pharyngeal muscles (arrowheads) lie between them; pedal glands are voluminous. B: Cartilage-like cells of radula bolster, *H. juani*, with small nuclei and attached muscles. C: Dorsal cecum of midgut, esophagus, radula, and large radula bolsters, *H. juani*; asterisks indicate lateral and ventral nerve cords. D: Radular sac, cross-section of proximal end, *H. juani*, with odontoblasts and membranoblasts; tooth initiation (asterisk) and secretory activity evident at distal end of odontoblasts; radular membrane (arrowheads) secreted by membranoblasts with smaller, more basal, and darker-staining nuclei than odontoblast cells; superior epithelium secretes denticles, secretory activity indicated by arrows at distal end of cells; thick basal lamina (double arrowhead) and muscle bands underlie radular sac. E: Radula bolster, *Scutopus robustus*, with herring-bone arrangement of fibers, probably collagenous; cells have central nuclei and peripheral mitochondria (arrowheads), are of different densities, and are probably interspersed by muscle fibers; connective tissue surrounds organ (arrow). F: Ventral salivary gland, *S. robustus*, with mucous vacuoles and microvilli (in cross-section) between areas of connective tissue (arrowhead). DC, dorsal cecum; ES, esophagus; F, foot; MB, membranoblast; MU, muscle of odontophore; N, nucleus; OB, odontoblast; OC, oral cavity; PG, pedal gland; PH, pharynx; R, radula; RB, radula bolster; SE, superior epithelium; T, tooth; VSG, ventral salivary gland. Scale bars: A, C = 100  $\mu\text{m}$ , B, D = 20  $\mu\text{m}$ , E = 10  $\mu\text{m}$ , F = 5  $\mu\text{m}$ .

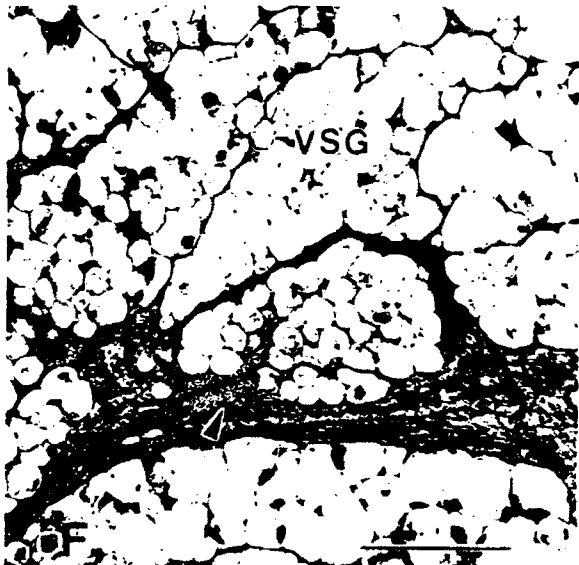
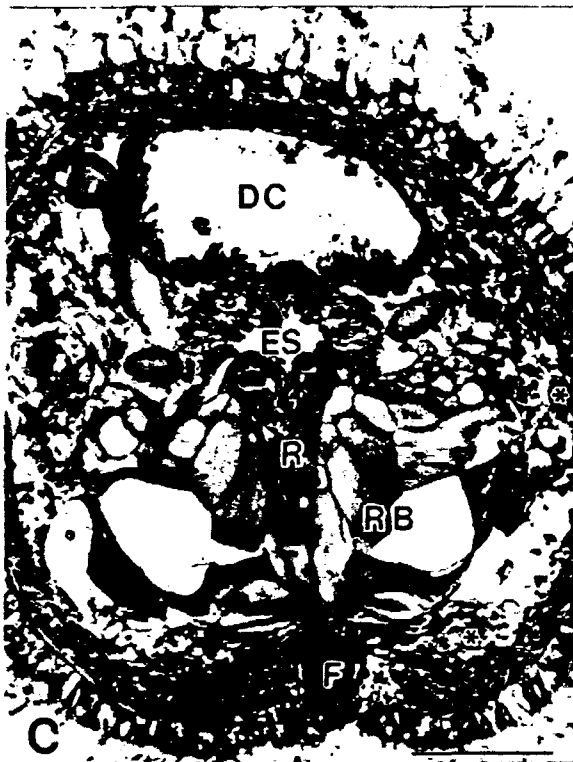
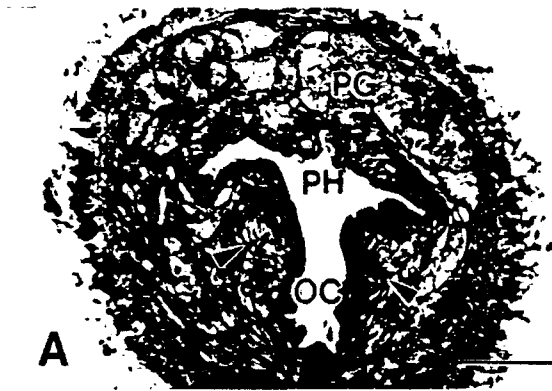


Figure 18. Radulae. A: Distichous radula, ventral view of distal end, *Scutopus robustus* (cf. Fig. 19). B: Highly derived distichous radula, *Chaetoderma argenteum*, with only two teeth on long cone-shaped piece connected to cuticular hood. (Photo J. Buckland-Nicks.) C: Polystichous radula, *Dorymenia* sp., cross-section of row with about 16 teeth on radular membrane; most teeth truncated by sectioning. D: Left side of distichous radula, *Helicoradomenia juani*, each tooth with 5 or 6 denticles. E: Distichous radula, ventral view, of a new genus, with distal ends turned into ventral pockets after radula opens into pharynx; pharyngeal cuticle remains after treatment. D, denticle; PH, pharynx; RM, radular membrane; T, tooth. Scale bars: A = 20  $\mu\text{m}$ , B, E = 100  $\mu\text{m}$ , C, D = 50  $\mu\text{m}$ .

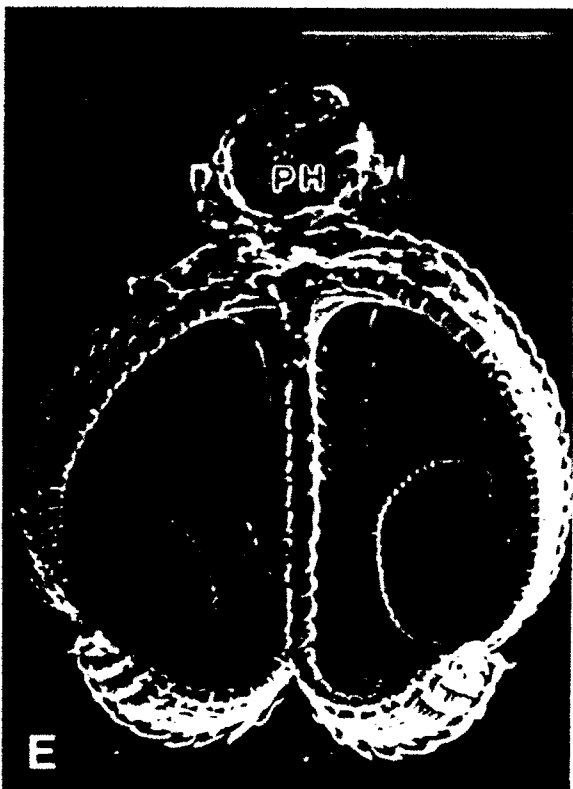
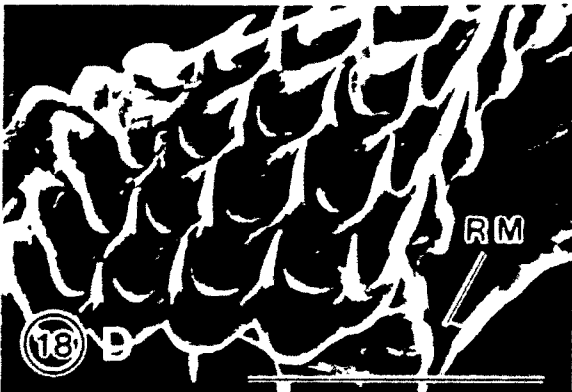
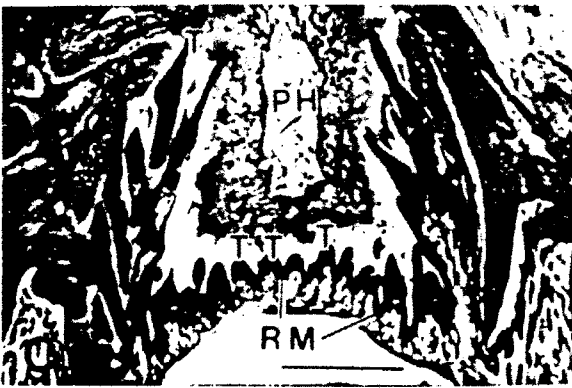


Figure 19. Cross-section, base of one row of distichous teeth, *Scutopus robustus* (cf. Fig. 18 A). Radular membrane attached to teeth by narrow band (arrowheads) beneath which membrane is darkly stained; membrane attached to inferior epithelium by microvilli (arrows). D, denticle; IE, inferior epithelium; RB, radula bolster; RM, radular membrane; T, tooth. Scale bar = 10  $\mu$ m.

TOP



Figure 20. Digestive system. A: Paired multicellular, simple ventral salivary glands and ducts (arrowheads), *Helicoradomenia juani*; one row of teeth (arrow) lies at entrance to ventral radular pocket. B: Paired intraepithelial salivary glands of *Limifossor talpoideus*, cells arranged around shared lumen (arrowheads); glands displaced dorsally by large odontophore. C: Proximal end of stomach of *Chaetoderma nitidulum canadense* with gastric shield (arrowhead). D: Style sac of *C. n. canadense* with food bolus (arrowhead) and mucoid rod (asterisk); digestive gland cells 1 and 2 enlarged in Figure 21 E,F. E: Midgut gland cells of *Eleutheromenia* sp. F: Midgut gland cells of *Helicoradomenia juani*. G: Midgut gland cells of *Ocheyoherpia* sp., three-layered body-wall musculature above (outer circular, middle orthogonal oblique, and inner longitudinal). C, cuticle; DG, digestive gland; MG, midgut; OD, odontophore; PH, pharynx; SG, salivary gland; ST, stomach; VSG, ventral salivary gland. Scale bars: A-D, G = 100  $\mu\text{m}$ , E, F = 20  $\mu\text{m}$ .



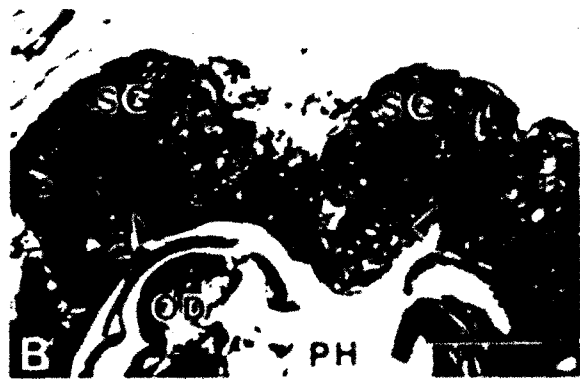
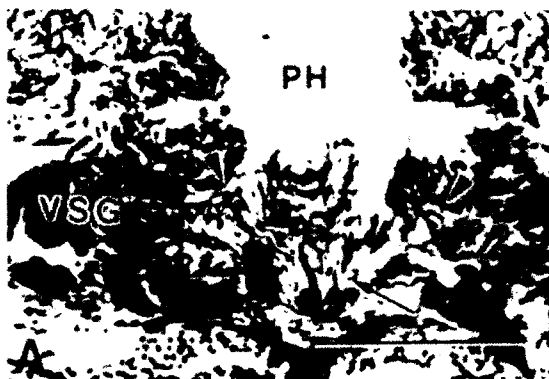


Figure 21. Digestive system. A: Oral cavity epithelium, *Micromenia fodiens*, deeply invaginated with brush border (arrowheads) and sensory cirri (arrow); muscle cells with strongly folded sarcoplasm and many mitochondria (asterisk) form base. (Photo K. Wolter.) B: Two nematocysts in pharynx, *M. fodiens*, one with empty appearance; pharyngeal cuticle polyciliated (arrowheads). (Photo K. Wolter.) C: Stomach epithelium, *Scutopus robustus*, with low cells, many lipid droplets and dark vesicles, a dense apical layer of fibers (arrow), and microvilli; basal lamina infolded. D, E: Digestive gland granules, *Scutopus ventrolineatus* (cf. Fig. 20 D, cell type 1); granule cells with laterally positioned nuclei, granules in different stages of development, membrane-bound vesicles (arrowheads), and rough endoplasmic reticulum; granules mineralized, with concentric dense layers surrounded by membrane. F: Club-shaped cell of digestive gland, *S. ventrolineatus* (cf. Fig. 20, cell type 2), with mineralized granules and glandular body in large apical vacuole; apical cell membrane will rupture and release glandular body into lumen of digestive gland; nuclei small, either lateral or basal. DG, digestive gland; GC, gland cell; HC, hemocoel; MU, muscle fibers, N, nucleus; NM, nematocyst; OC, oral cavity; PH, pharynx; RER, rough endoplasmic reticulum; ST, stomach. Scale bars: A, C, E, F = 10  $\mu\text{m}$ , B = 5  $\mu\text{m}$ , D = 1  $\mu\text{m}$ .

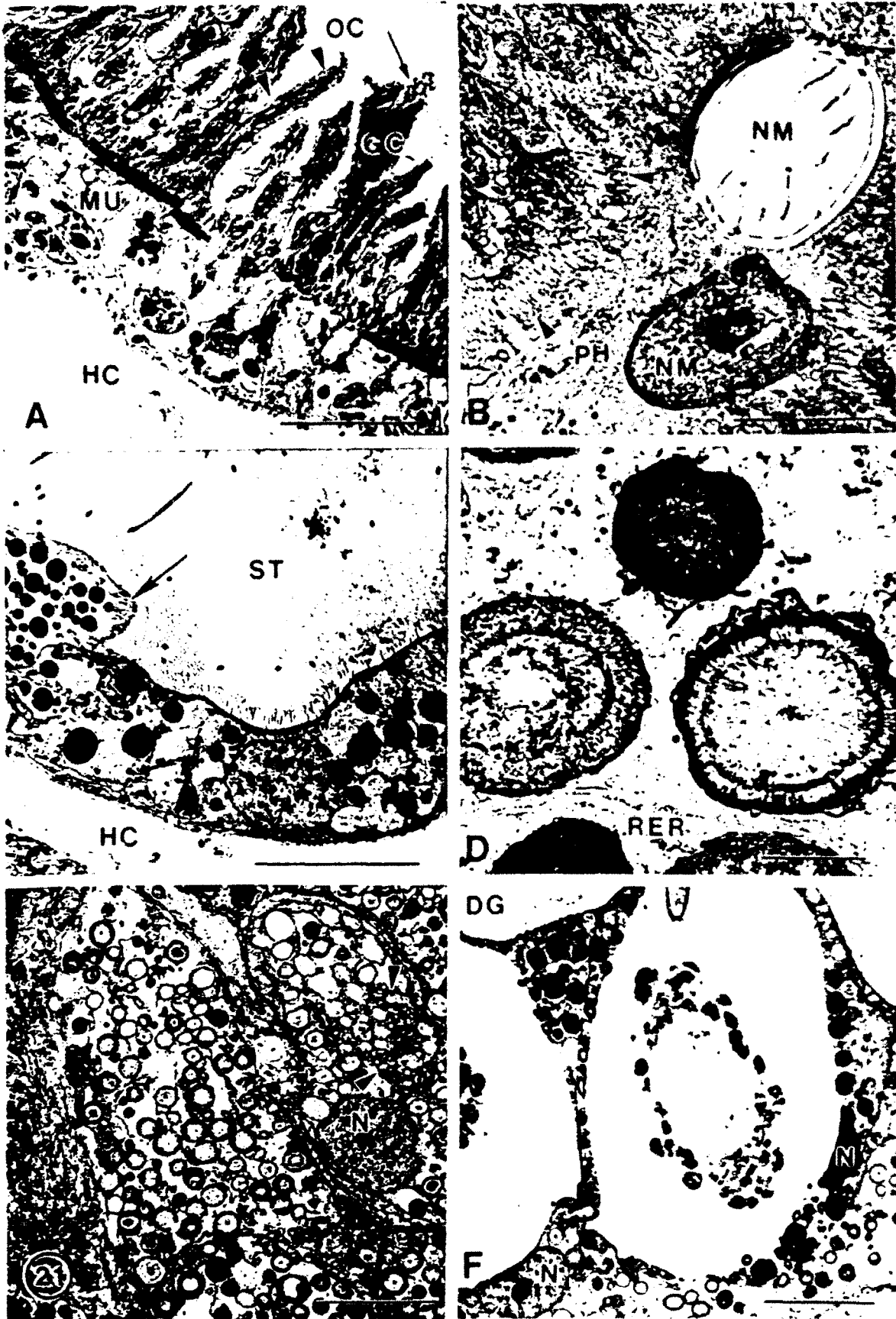


Figure 22. Heart, pericardium, and reproductive system. A: Heart, *Chaetoderma nitidulum canadense*; auricle opens from blood-cell filled sinus (asterisk) at base of ctenidia, in which lie gill retractor muscles; ventricle with strong musculature leads to aortal bulb (arrowhead) (cf. Fig. 14). B: Heart, *Helicoradomenia juani*, free in mantle cavity (cf. Fig. 23 F); auricle opens into ventricle with weak musculature. C: Ciliated posterior end of pericardial cavity, *H. juani*, leading to upper gametoduct; auricle is invagination of pericardial wall, opens dorsally to hemocoel; suprarectal commissure lies above rectum. D: Mature ovum without nuclear membrane in pericardium, *H. juani*; lateral ciliated tract of pericardial wall (arrowheads) directs gametes posteriorly through pericardium. E: Seminal vesicles, *Dorymenia* sp., with endogenous spermatozoa in pockets of upper gametoduct (cf. Fig. 24 G). F: Seminal receptacle, *H. juani*, with long duct to lower gametoduct (cf. Fig. 24 F); adjacent decalcified copulatory spicules are surrounded by two sets of muscle bands. AU, auricle; CS, copulatory spicule; CT, ctenidium; GD<sub>1</sub>, upper gametoduct; GD<sub>2</sub>, lower gametoduct; HC, hemocoel; MG, midgut; MU, muscle; OV, ovum; PC, pericardial cavity; RE, rectum; SC, suprarectal commissure and ganglion; SR, seminal receptacle; SV, seminal vesicle; V, ventricle. Scale bars: A = 200  $\mu$ m, B, D. = 20  $\mu$ m, C, F = 100  $\mu$ m, E = 50  $\mu$ m.

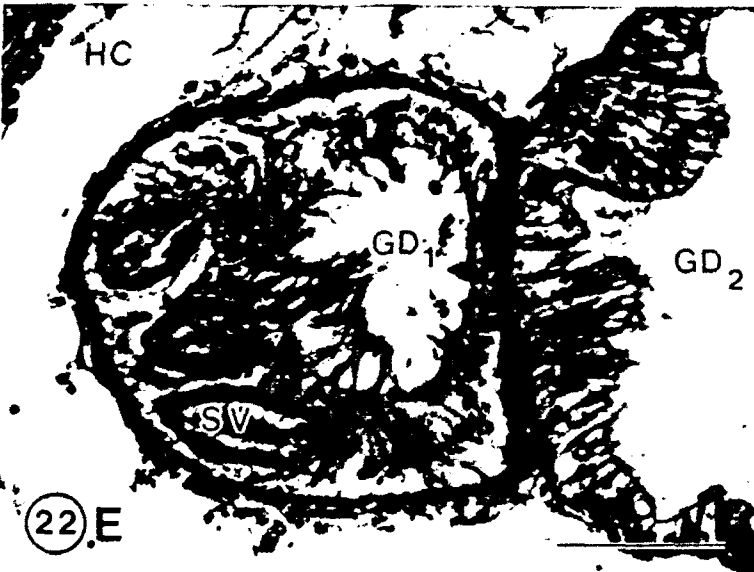
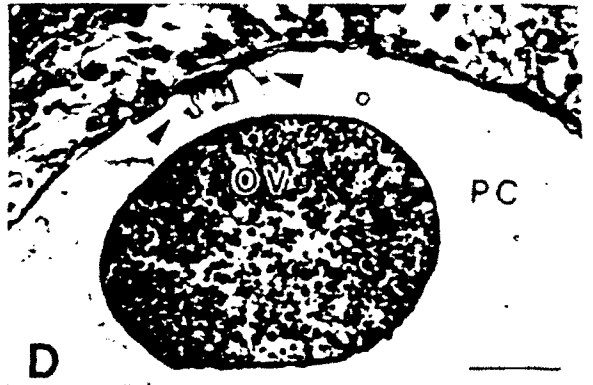
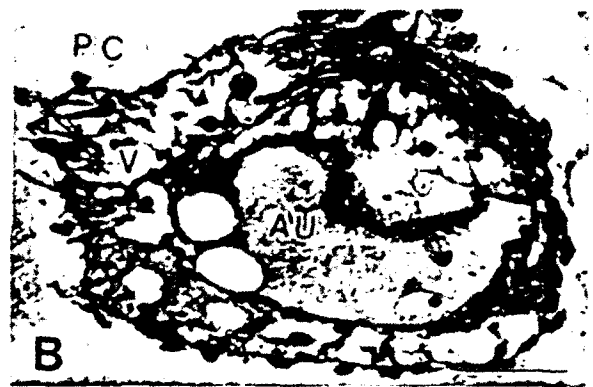
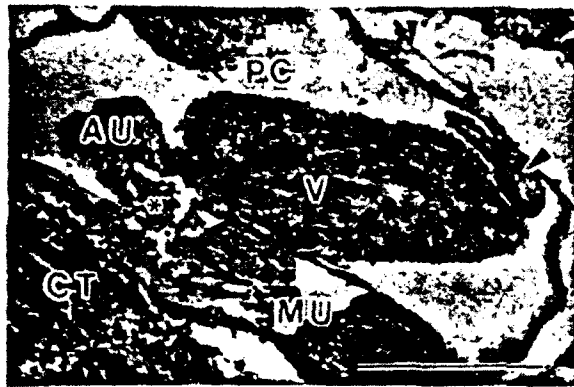


Figure 23. Reproductive system. A: Matrix of unpaired copulatory spicules in pocket and copulatory spicule gland, *Lyratoherpia* sp. (cf. Fig. 24 B, H); lower gametoducts are narrow. B: Spermatophore in lower gametoduct, *Gymnomenia* sp; gametoduct surrounded by muscle band (arrowhead). C: Copulatory spicule pocket, *Helicoradomenia juani*, one of pair, membranous matrix (arrowheads) indicates 2 spicules present (cf. Fig. 24 C; section midway between Figs. 22 F and E below). D: Paired copulatory pockets, *Gymnomenia* sp., with copulatory spicule glands and matrices (asterisks) of more than 12 dissolved spicules per group (cf. Fig. 24 A). E: Paired copulatory spicule pockets, *H. juani*, with copulatory spicule glands, section posterior to C above; lower gametoducts united here before emptying into mantle cavity further posteriorly. F: Ova in pericardium, *Dorymenia* sp., with thick, irregular outer membranes; heart attached dorsally for entire length to pericardial wall. G: Lower gametoduct, *Facidens crossotus*; cells with large vacuoles, one enclosing an electron-dense secretion (arrow), and small basally situated nuclei; arrowheads indicate basal membrane labyrinths. H: Oocyte in hermaphroditic gonad, *Micromenia fodiens*, with two nucleoli and membrane-bound vesicles; nuclear membrane and nucleoli will dissolve before ovum reaches pericardium; spermatocytes indicated by arrowheads. (Photo K. Wolter.) C, cuticle; CS, copulatory spicule; CSG, copulatory spicule gland; DS, dorsal sinus; GD<sub>2</sub>, lower gametoduct; N, nucleus; NL, nucleolus; OV, ovum; PC, pericardial cavity; V, ventricle. Scale bars: A, C, E, F = 100  $\mu\text{m}$ , B, D = 20  $\mu\text{m}$ , G = 5  $\mu\text{m}$ , H = 10  $\mu\text{m}$ .

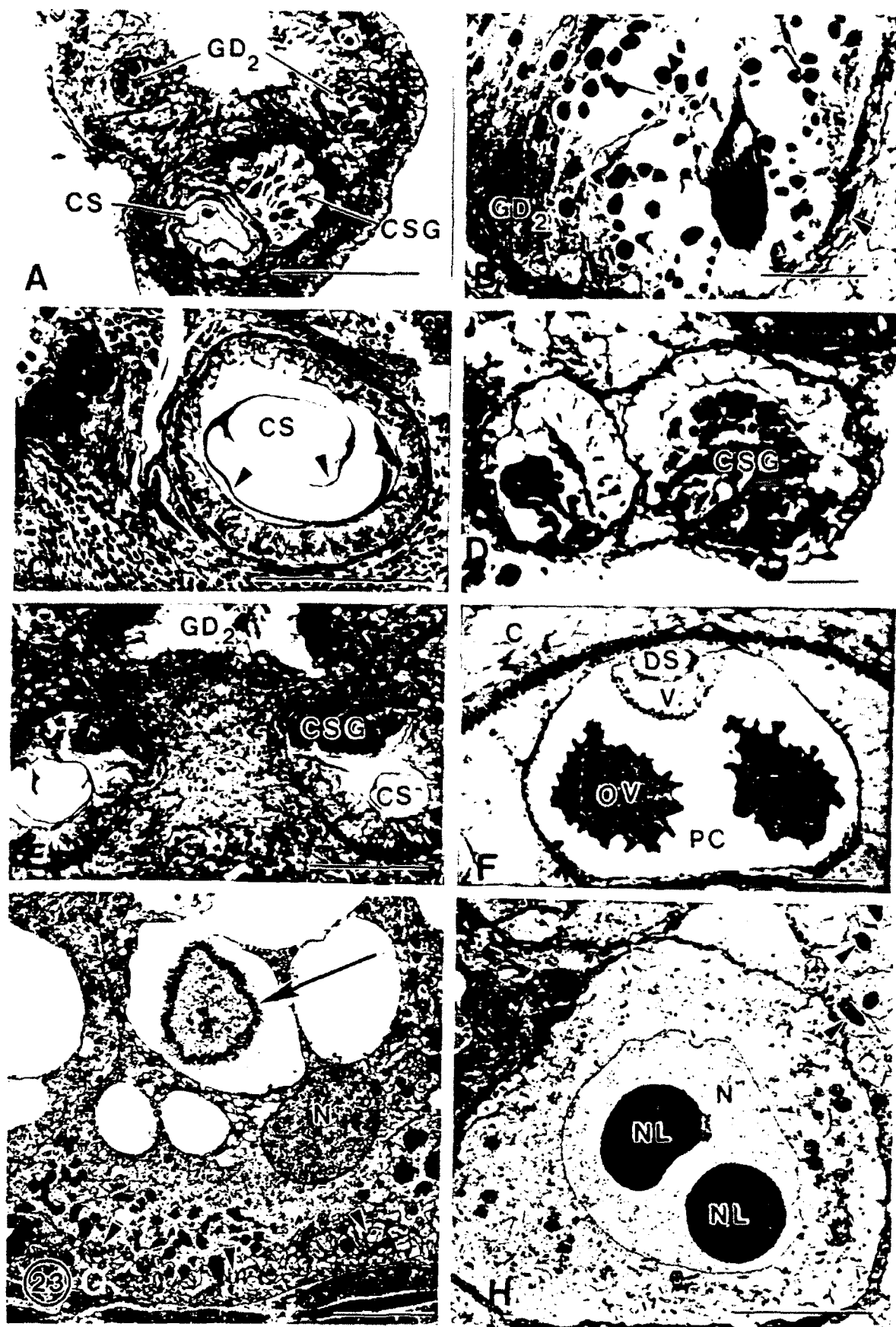


Figure 24. Neomenioid reproductive system. A-E: Calcareous copulatory spicules, distal end upward. F-I: Schematic lateral views of duct system: gonad, pericardial cavity, upper (1) and lower (2) gametoducts, seminal vesicle, seminal receptacle, and copulatory spicule gland and spicules; gametopore and copulatory spicules enter mantle cavity to right.

A: *Gymnomenia* sp., 4 of several fluted, hollow, probably deciduous spicules per copulatory spicule pocket. B, H: *Lyratoherpia* sp., highly derived reproductive system with single copulatory spicule pocket within large, tubular copulatory spicule gland which externally forms bulge seen below mantle cavity (cf. Figs. 3 B, 23 A); single group of solid spicules, tips of 2 longest broken off; seminal vesicle large, leading from anterior pericardial cavity to short, ventrally directed upper gametoduct; seminal receptacle bilobed. C, F: *Helicoradomenia juani*, one of paired group of two spicules (cf. Figs. 22 F, 23 C, E) and one accessory spicule of paired group of two; upper gametoduct narrow, long, communicates with posterior part of seminal receptacle just anterior to long duct leading dorsally from seminal receptacle to lower gametoduct (cf. Fig. 22 F). D: *Eleutheromenia* sp., hooded spicule, one of pair, spicule length 1/4 to 1/3 total body length (cf. Fig. 3 A). E, G: *Dorymenia* sp., one of paired, twisted spicules with high organic content and one of numerous accessory spicules (cf. Fig. 11 C); seminal vesicle as evaginated pockets of upper gametoduct (cf. Fig. 22 E). I: *Strophomenia scandens* Heath, with many-lobed seminal receptacle (after Heath, 1911). CS, copulatory spicule; CSG, copulatory spicule gland; G, gonad; PC, pericardial cavity; SR, seminal receptacle; SV, seminal vesicle. Scale bars: A, B = 50  $\mu$ m, C-E = 100  $\mu$ m.



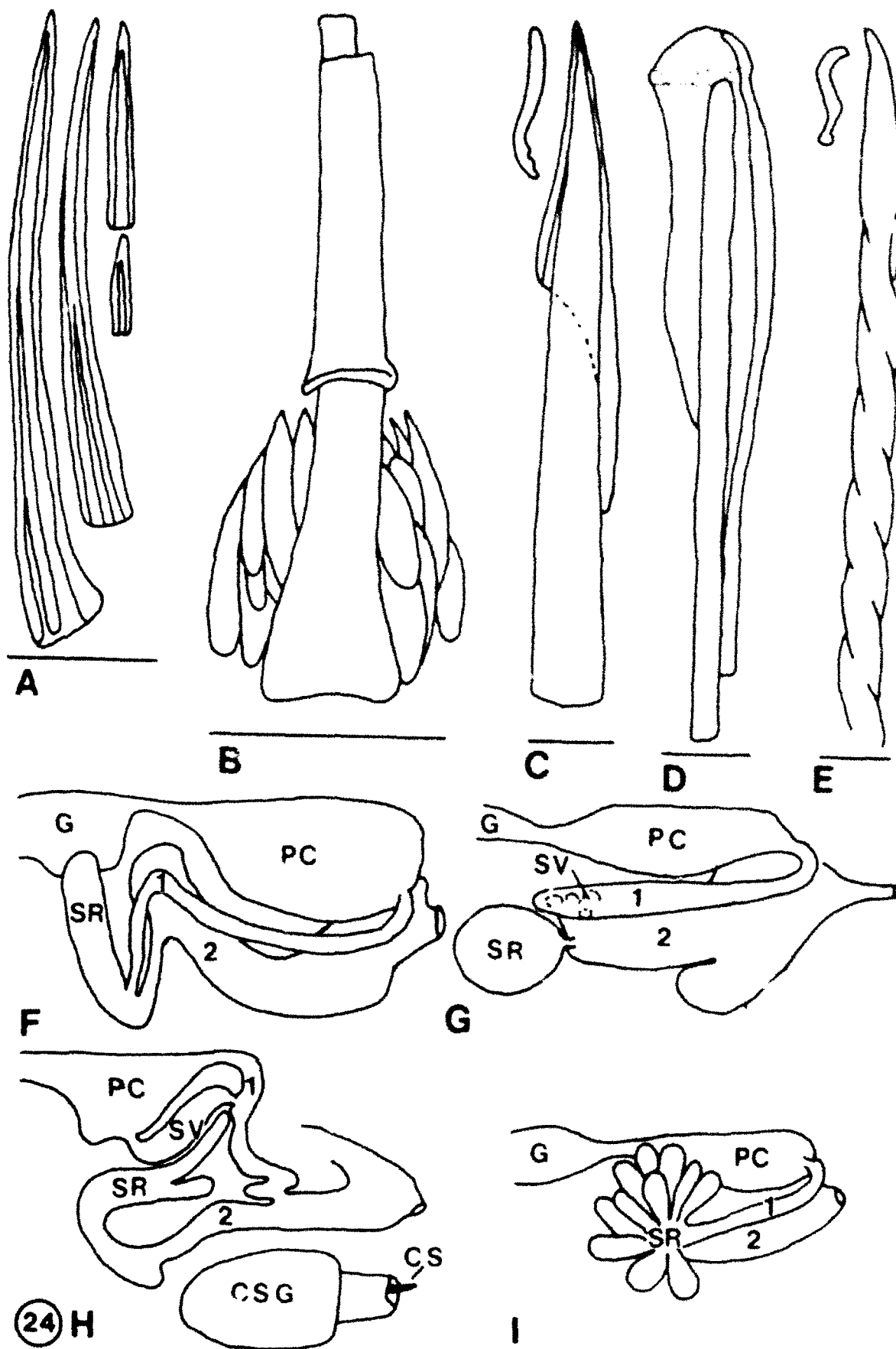
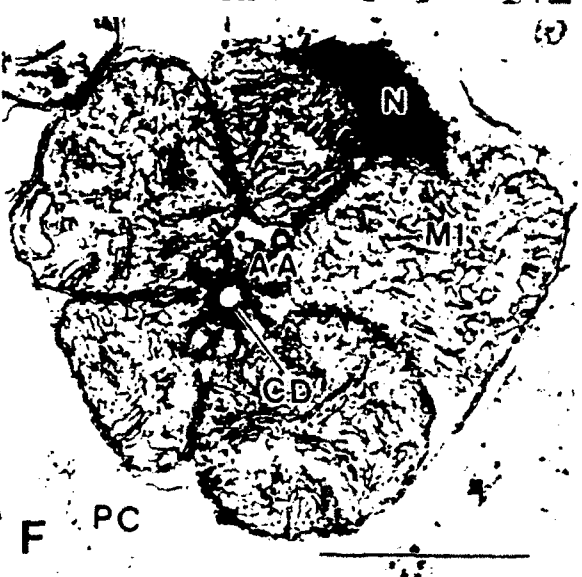
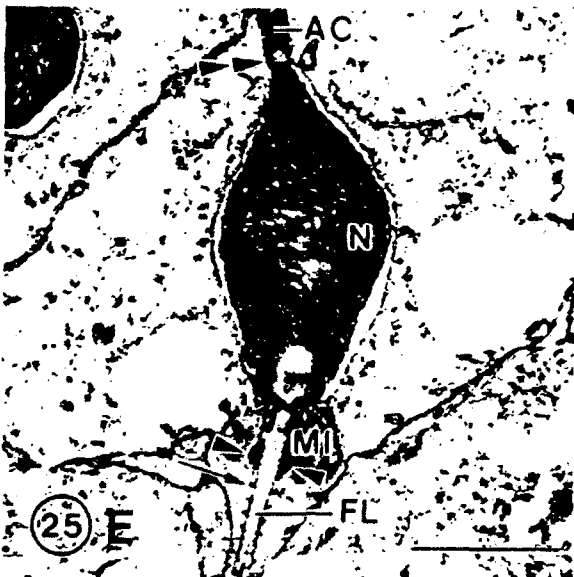
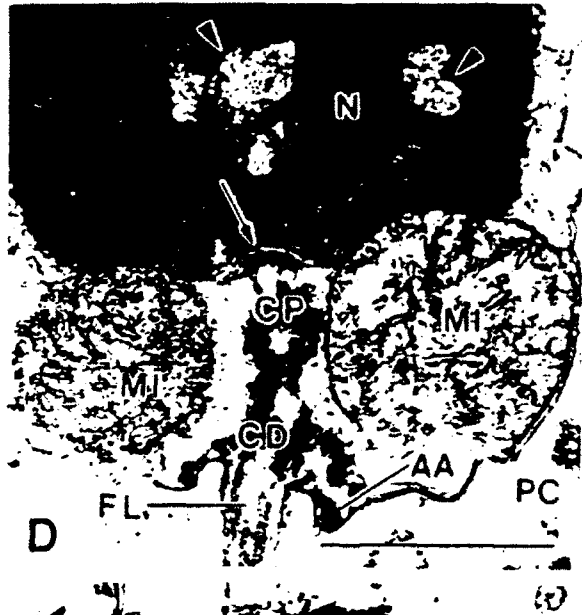
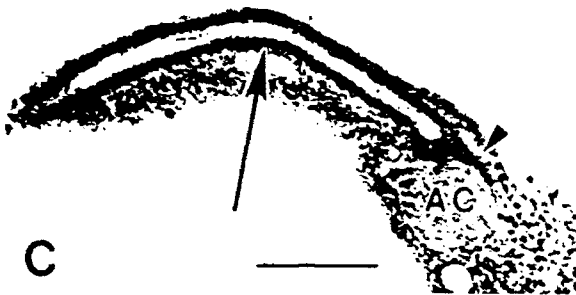
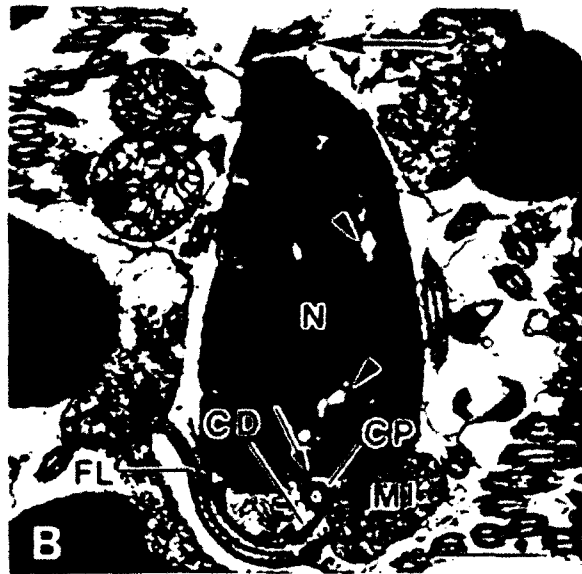
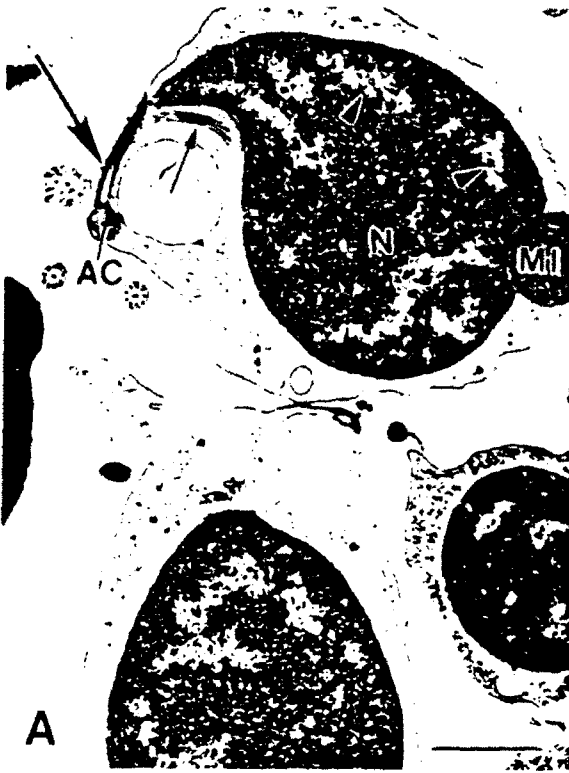


Figure 25. Reproductive system, male gametes. A: Spermatid, *Chaetoderma argenteum*, nucleus pear-shaped; condensed granules of chromatin leave lacunae (arrowheads); Golgi body (small arrow) responsible for secretion of pro-acrosomal granule lies between large vesicle and indentation of nucleus; pro-acrosome in contact with tip of apical dense tube (large arrow) which will break free of cytoplasm. (From Buckland-Nicks and Chia, 1989.) B: Spermatozoon, *Scutopus ventrolineatus*, nuclear chromatin further condensed than A, some lacunae (arrowheads) remain; distal, dense tube (arrow with question mark) may be present, homologous to that in *Chaetoderma* (A, C); basal plate (arrow) lies proximally. C: Apical dense tube (arrow) with no nuclear material bearing acrosome at its apex not yet entirely free of cytoplasm; finger-like process of tube extends above acrosome (arrowhead). (From Buckland-Nicks and Chia, 1989.) D, F: Mid-body of spermatozoon in pericardial cavity, *S. ventrolineatus*, transverse and cross-sections; five spherical mitochondria with tubular cristae symmetrically arranged, indenting base of nucleus; between fossae lies basal plate (arrow); proximal and distal centrioles centrally situated perpendicular to each other, flagellum or tail extends centrally from distal centriole; centriolar satellite complex with primary and secondary processes anchors distal centriole to plasma membrane. E: Spermatozoon, *Micromenia fodiens*, with distal tube of acrosome above subacrosomal space (double arrowheads); nucleus with chromatin condensed into twisted fibers; nuclear fossa large; midpiece with only two mitochondria; dark annulus (arrowheads) around flagellar base; helicoid strand (arrow) wraps around flagellum. (Photo K. Wolter.) AA, anchor apparatus; AC, acrosome; CD, distal centriole; CP, proximal centriole; FL, flagellum; MI, mitochondrion; N, nucleus; PC, pericardial cavity. Scale bars: A, B, D-F = 1  $\mu\text{m}$ , C = 0.4  $\mu\text{m}$ .





# *Helicoradomenia juani* gen. et sp. nov., a Pacific Hydrothermal Vent Aplacophora (Mollusca: Neomeniomorpha)

by

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**Abstract.** The aplacophoran *Helicoradomenia juani* gen. et sp. nov. is found in large numbers at the northeast Pacific vent sites of Juan de Fuca Ridge, Explorer Ridge, and Gorda Ridge. It is placed in the family Simrothiellidae on the basis of radular morphology (distichous bars with paired ventral pockets) and is separated from other genera in the family by the presence of solid epidermal spicules.

## INTRODUCTION

Several closely related species of neomenioid (footed) Aplacophora occur at hydrothermal vents. They were originally assigned to the genus *Simrothiella* Pilsbry, 1878 (SCHELTEMA, 1988; TURNER, 1985, through personal communication from Scheltema), but re-examination of type material of *S. margaritacea* (Koren & Danielssen, 1877) indicates that the latter is generically distinct from the hydrothermal vent species on the basis of the radula alone (cf. Figure 2D, E). The type species for the new genus is described here.

## MATERIALS AND METHODS

All specimens (365) were collected from the Endeavour segment of Juan de Fuca Ridge (47°57'N, 129°04'-06'W, 2250 m), Explorer Ridge (49°46'N, 130°16'W, 1800 m), and Gorda Ridge (41°00'N, 127°30'W, 3271 m) from the deep submersible research vessels *ALVIN* and *PISCES*.

About 20 specimens were dissected or sectioned. Radulae, epidermal spicules, and copulatory spicules were dissociated from dissected anterior or posterior ends of specimens by dissolving tissue in hypochlorite solution (household bleach) or, for some radulae, in 10% NaOH solution. They were washed and placed in a drop of glycer-

ine for camera lucida drawing. After further washing, permanent slides were made of air-dried spicules and CMCP-10 (TURTOX)-mounted radulae. One specimen was prepared for histology by decalcifying the spicules with 0.5 M EGTA overnight, dehydrating in dimethoxy propane, and embedding in epon/araldite epoxy resin. Sections were cut at 1.5  $\mu$ m and stained with Richardson's stain (azure II and methylene blue). Standard paraffin sections (7  $\mu$ m) were also cut and stained with Mallory-Heidenhain trichrome. Types are deposited in the National Museum of Natural History (NMNH), Washington, DC.

**Terminology:** *Skeletal (=tangential) spicules* are those that lie within the cuticle and spiral around the body at a 45° angle, crossing each other at 90°; *upright (=radial) spicules* extend out of the cuticle; *isochromes* are boundaries between color bands produced in solid spicules by cross-polarized light; *distichous* refers to a radula formed by repeated rows of two teeth each (formula: number of rows  $\times$  1:1); *denticulate bar* is a bar-like radular tooth with denticles on the side opposite to the attachment of the tooth to the radular membrane; *vestibule (=atrium)* is the anterior cavity that lies above the mouth either united with or separate from the mouth opening and that contains sensory papillae; *oral cavity (=buccal cavity)* is the ventral space into which the mouth opens and which leads dorsally to the *pharynx*.

## SYSTEMATICS

Subclass Neomeniomorpha Pelseneer, 1906

Ventroplicida Boettger, 1956

Solenogastres Gegenbaur, 1878 (*partim*), Salvini-Plawen, 1967

Aplacophoran mollusks with a narrow foot in a ventral furrow, an anterodorsal vestibule with sensory papillae, a combined stomach-midgut gland, serial lateroventral muscles, a mantle cavity without ctenidia, and paired hermaphroditic gonads.

Family SIMROTHIELLIDAE

Salvini-Plawen, 1978

**Type species:** *Solenopus margaritaceus* Koren & Danielsen, 1877.

Radula with distichous denticulate bars and short or long paired anteroventral radular pockets; spicules hollow or solid; skeletal spicules present or absent; morphology of ventral salivary glands varied.

*Helicoradomenia* Scheltema & Kuzirian,  
gen. nov.

Plump to somewhat elongate, nearly smooth to spiny, 5 mm or less in length, dorsoposterior sense organ and sometimes dorsofrontal sensory pit present; proboscis large, protrusible; mouth at proximal end of vestibule; pedal pit large, often protruded; cuticle thin, epidermal glands not stalked; spicules solid, upright, skeletal spicules lacking; radula large, lateral denticles longest; radula spiraling into paired anteroventral radular pockets, first-formed teeth not retained; paired ventral salivary glands small, opening through paired ducts; paired sac-like seminal receptacles; single gametopore; copulatory spicule pockets paired, 2 or more long spicules per pocket; mantle cavity with long respiratory papillae.

**Range:** Eastern and western Pacific hydrothermal vents.

**Etymology:** *helico* = helical, *rad* = abbreviation for radula, *menia* = moon, usual ending for neomenioid ("new moon") aplacophorans.

*Helicoradomenia juani* Scheltema & Kuzirian,  
sp. nov.

(Figures 1-5)

**Holotype:** 3.4 mm long, anterior diameter 0.7 mm, midbody 1.0 mm, posterior 1.6 mm. Endeavour Segment, Juan de Fuca Ridge, 47°57'N, 129°04'W, 2250 m (DSRV *ALVIN* Dive 1419). NMNH No. 836328.

**Figured paratypes:** Nos. 1, 3, 6, 9, 14, from type locality NMNH Nos. 860188, 860187, 860191, 860189, and 860190, respectively.

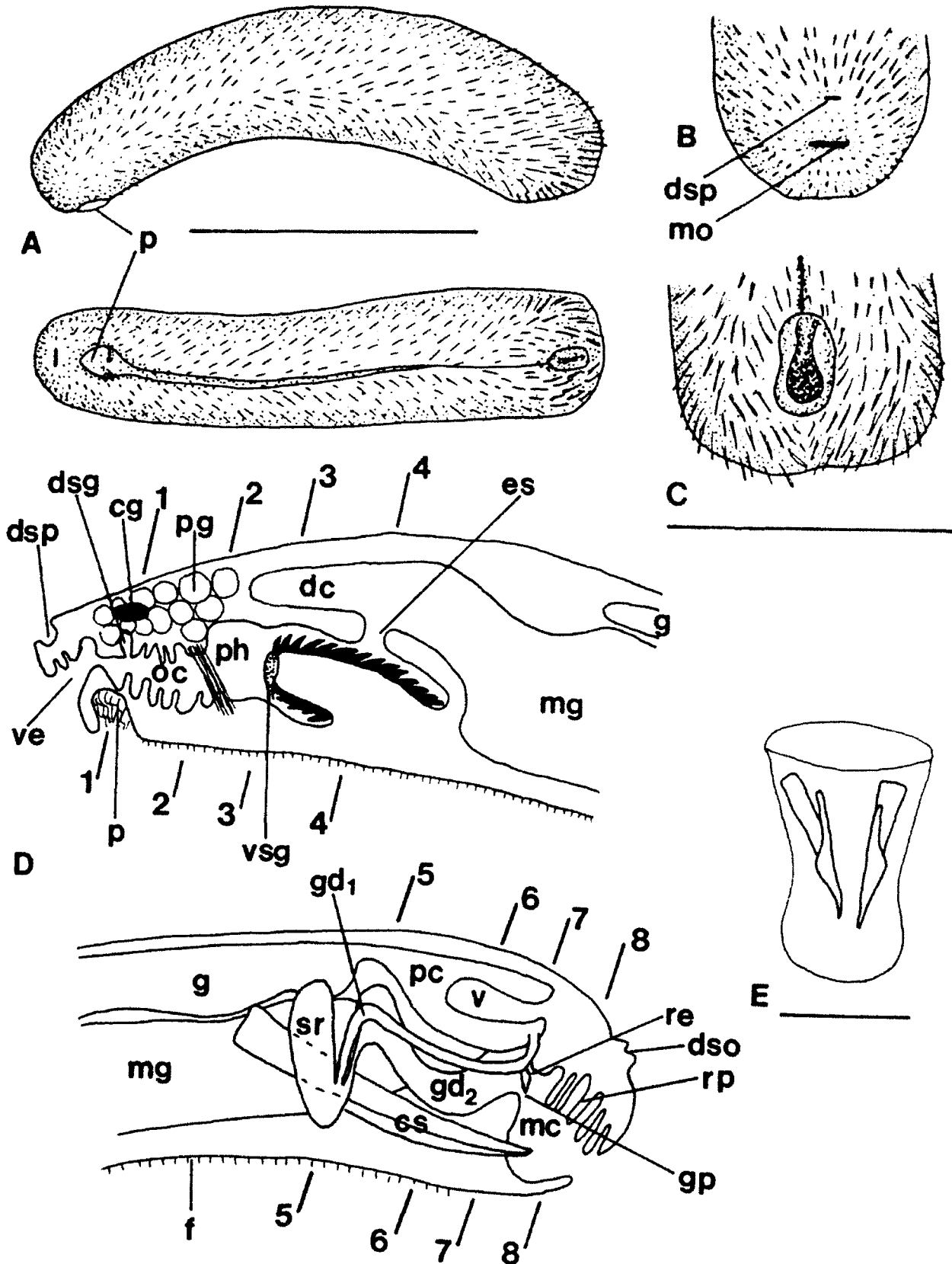
**Distribution:** Explorer, Juan de Fuca, and Gorda ridges, 1800-3271 m.

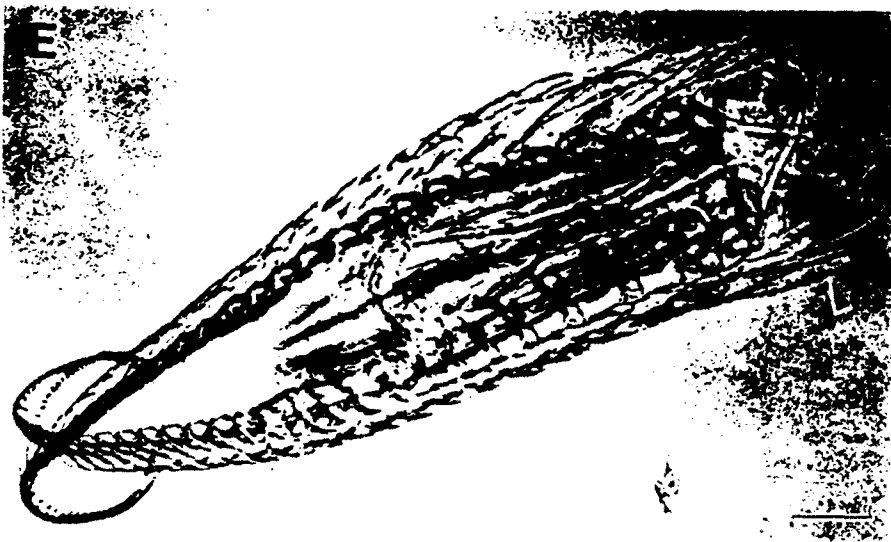
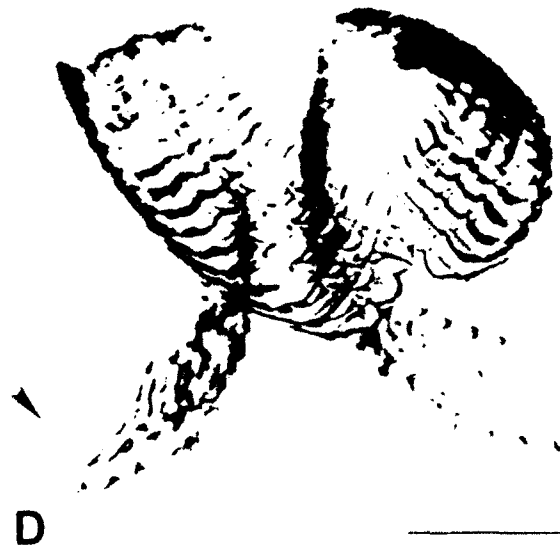
**Diagnosis:** Appearance fuzzy, length to 5 mm, narrowest anteriorly, mean index (length:diameter) at midbody 4.1; with dorsofrontal sensory pit; spicules widest at base and distally pointed, varying from short, wide, and recurved (110  $\mu$ m long, 18  $\mu$ m wide, 10  $\mu$ m thick) to long, slender and curved (200  $\mu$ m long, 14  $\mu$ m wide, more than 10  $\mu$ m thick); radular formula 34-35  $\times$  1-1, teeth with 5 or 6 denticles, lateral denticle twice length of next adjacent one; 2 spicules per copulatory spicule pocket, curved, sharply pointed distally, up to 1 mm long, shorter spicule of pair with proximal process; accessory copulatory spicules 2 on each side, with 3 low bumps.

**External anatomy and hard parts:** Body (Figures 1A-C, 2A) somewhat elongate, index at midbody 3-4.1; anterior end rounded; wider posterior end slightly pointed with flattened ventral region around mantle cavity opening; mouth slit lateral; dorsofrontal sensory pit obvious as lateral slit; dorsoterminal sense organ not evident externally; mantle cavity opening axial, oval. Epidermal spicules (Figure 3A, B) of 5 types, longest at posterior end of body, usually thickest near base: (1) evenly curved, narrow, width even except tapered distally to point, up to 130  $\mu$ m long  $\times$  11  $\mu$ m wide, 7  $\mu$ m to more than 10  $\mu$ m thick, grades into (2) straight or evenly curved, width even except expanded basally and tapered distally to blunt point, up to 200  $\mu$ m long  $\times$  15  $\mu$ m wide, more than 10  $\mu$ m thick; (3) broad, base recurved proximal to indentation or unevenly curved, distally tapered to point, up to 112  $\mu$ m long  $\times$  18

Figure 1

*Helicoradomenia juani* gen. et sp. nov. A: Holotype, showing spicule orientation and somewhat protruded pedal pit, lateral (above) and ventral views. B: Holotype, anterior end, frontal view showing relationship of dorsofrontal sensory pit and opening to mouth and vestibule. C: Holotype, posterior end, ventral view, with oval-shaped mantle cavity opening. D: Schematic sagittal sections of anterior (above) and posterior ends; transverse sections 1-8 are keyed to histologic sections in Figures 4 and 5. E: Copulatory spicules *in situ*, paratype no. 3, ventral view of posterior end (rotated 90° from D, mantle opening below), tissue partially dissolved. Key: cg, cerebral ganglion; cs, copulatory spicule; dc, dorsal cecum; ds, dorsal salivary gland; dso, dorsoterminal sense organ; dsp, dorsofrontal sensory pit; es, esophagus; f, foot; g, gonad; gd<sub>1,2</sub>, upper and lower gametoducts; gp, gametopore; mc, mantle cavity; mg, midgut (stomach-intestine); mo, opening to vestibule and mouth; oc, oral cavity; p, pedal pit; pc, pericardial cavity; pg, pedal gland; ph, pharynx; re, rectum; rp, respiratory papilla; sr, seminal receptacle; v, ventricle; ve, vestibule; vs, ventral salivary gland. Scale bars: A = 2.0 mm, B, C = 1.0 mm, E = 0.05 mm.







$\mu\text{m}$  wide, 9  $\mu\text{m}$  or less thick; (4) short, straight, rounded basally, tapered distally to point, up to 74  $\mu\text{m}$  long  $\times$  15  $\mu\text{m}$  wide, 7  $\mu\text{m}$  or less thick; (5) short, straight or curved, distally pointed, base straight, up to 80  $\mu\text{m}$  long  $\times$  11  $\mu\text{m}$  wide, 9  $\mu\text{m}$  or less thick. Pedal-groove spicules short and broad, up to 70  $\mu\text{m}$  long  $\times$  16  $\mu\text{m}$  wide, 4–5  $\mu\text{m}$  thick.

Copulatory spicules (Figures 1D, E, 3D, E, 5C) 2 per pocket, curved dorsally, sharply pointed distally, longer spicule up to 1 mm in length with straight base, shorter spicule with proximal process, medioventral to and partially wrapped around longer spicule. Paired accessory spicules (Figures 3C, 5G) 2 on each side, recurved, each with 3 low bumps on base.

Radula (Figures 2B, D, 3F, G) with single turn into ventral pockets; 34 or 35 rows; teeth with 5 or 6 denticles, lateralmost denticle twice length of next adjacent denticle; bar about 115  $\times$  12  $\mu\text{m}$ , lateral denticle 30  $\mu\text{m}$ ; dimensions of older teeth smaller.

**Internal anatomy (Figure 1D):** Cuticle 22  $\mu\text{m}$  thick. Epidermis (Figure 2C) 22  $\mu\text{m}$  thick, with more than one type of secretory cell, pierced by tubules from hemocoel. Body-wall musculature well developed. Pedal pit lined by large secretory cells (Figure 4A). Vestibule with few low, broad papillae; cirri grouped at mouth opening with which vestibule is united. Oral cavity deeply folded, also with cirri (Figure 4A). Multicellular dorsal salivary gland small (Figure 4A). Pharyngeal wall smooth (Figure 4B). Ventral salivary glands paired, small, tube-shaped, multicellular, unbranched, non-basophilic staining (Orange G), each opening through separate duct into anterior end of anteroventral radular pocket (Figure 4C). Anteroventral radular pocket as paired pouches which remain connected medially for some distance (Figure 4C). Radula bolsters large, bolster muscles well developed (Figure 4D). Short esophagus present (Figure 4D). With single, short dorsal midgut cecum (Figure 4D); midgut sacculate. Pericardial cavity large (Figure 5C); heart large, free within pericardium, opening from a posterior dorsal sinus (Figure 5C, D). Seminal receptacles as paired, large tubes lying in a dorsoanterior to ventroposterior position, each opening through a narrow tube leading dorsally to lower gametoduct (Figure 5A, B). Upper gametoduct opens into sem-

inal receptacle through a narrow duct adjacent to the tube joining the seminal receptacle and lower gametoduct (Figure 5B). Gametopore single, opening into mantle cavity below rectum (Figure 5E). Mantle cavity with numerous long respiratory papillae (Figure 5F). Dorsoterminal sense organ large, papillate, seen only in sectioned material.

**Remarks:** The reproductive system of these animals is unusual because (1) the upper gametoduct is joined to the distal end of the seminal receptacle rather than to the lower gametoduct, and (2) the position of the tubes connecting the seminal receptacles to upper and lower gametoducts is asymmetrical, being medial to the copulatory spicules on the left side and lateral to them on the right side in the specimen sectioned (Figure 5A, B).

The ventral salivary glands are embedded in the muscles of the radula (Figure 4C). They are unusually small and do not have a basophilic reaction to trichrome staining. This condition is atypical from the strong basophilia found in the salivary glands of most other neomenioids and presumably reflects diet. Nematocysts were not found in the midgut of *Helicoradomenia juani*, and Cnidaria did not occur where this species was collected. It is thus assumed that *H. juani* is not a cnidarivore as are most neomenioids. The organic matter seen in the gut has not been identified.

**Relationships:** Isolated radulae have been examined from three genera belonging to the family Simrothiellidae Salvini-Plawen: *Simrothiella* Pilsbry, 1898 (Figure 2E), *Kruppomenia* Nierstrasz, 1903a (synonymy with *Simrothiella*, SALVINI-PLAWEN, 1978, in error), and a new genus to be published which will include "*Simrothiella*" *schizoradulata* Salvini-Plawen, 1978. All have distichous bars and short to very long paired anteroventral radular pockets. It is this radular morphology that is the basis for placing *Helicoradomenia* in the Simrothiellidae. The epidermal spicules provide a basis for generic separation. In *Helicoradomenia* they are solid and thus differ from the hollow spicules found in all other genera in the family, which also includes *Cyclomenia* Nierstrasz, 1902, *Uncimenia* Nierstrasz, 1903b, *Birasoherpia* Salvini-Plawen, 1978, *Buseramenia* Salvini-Plawen, 1968, and *Sialoherpia* Salvini-Plawen, 1978. Although the illustrated radulae of these

Figure 2

A–D. *Helicoradomenia juani*. A: Holotype, anterior to left (cf. Figure 1A). B: Scanning electron photomicrograph of part of left half of radula from above, medial edge to left, paratype no. 6; five rows of teeth, some with five and some with six denticles, shown. Arrowhead indicates longest, most lateral denticle. C: Light micrograph of histologic section of epidermis and cuticle (c) of mantle showing various gland cells and innervation by nerve fibers (arrowhead). D: Light micrograph of entire radula from below showing helical position of teeth from anteroventral radular pocket, paratype no. 14; newest tooth indicated by arrowhead. E: Light micrograph of radula of *Simrothiella margaritacea* (Koren & Danielssen, 1877), ventral view with elongated paired ventral radular pockets to left and long lateral teeth (arrowhead) extending into pharynx on right (R. V. Chain 106 Sin 316, 50°58.7'N, 13°01.6'W, 2173 m). Species determination from comparison with radula isolated from a syntype, Bergen Museum no. 2078. Scale bars: A = 2.0 mm; B, C = 0.02 mm; D, E = 0.1 mm.

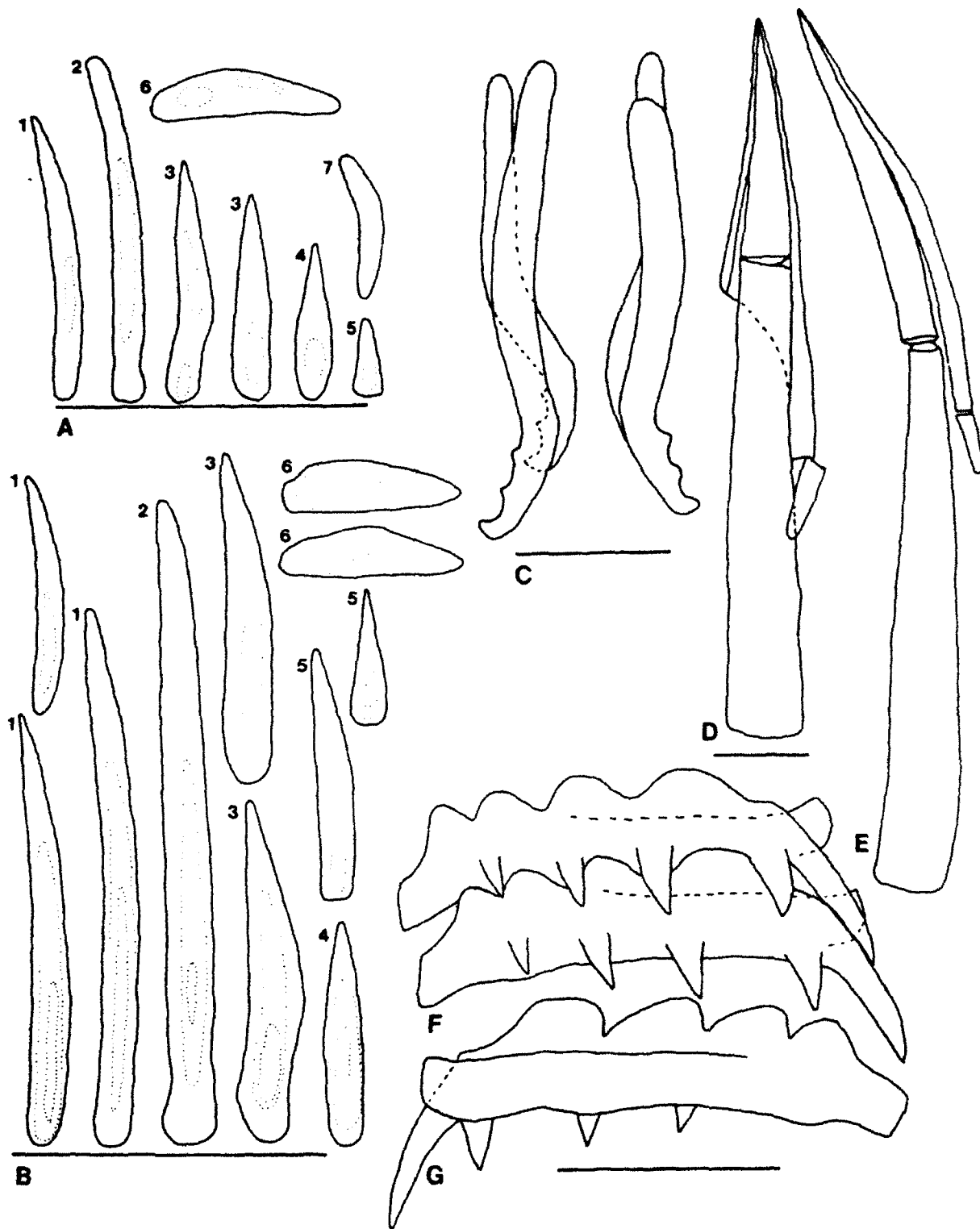


Figure 3

*Helicoreadomenia juani*, hard part morphology. A, B: Epidermal spicules, anterior and posterior, respectively, paratype no. 1; selected isochromes indicated by dotted lines; 1-5, see text; 6, pedal-groove spicules; 7, oral spicule. C: Accessory copulatory spicules, paratype no. 1 (cf. Figure 5G). D, E: Copulatory spicules from paratype nos. 1 and 9, respectively. F: Two adjacent teeth from right side of radula, paratype no. 1. G: Single radular tooth, right side, paratype no. 1, view from beneath radular membrane showing bar. Scale bars: A, B, D, E = 0.1 mm; C, F, G = 0.05 mm.

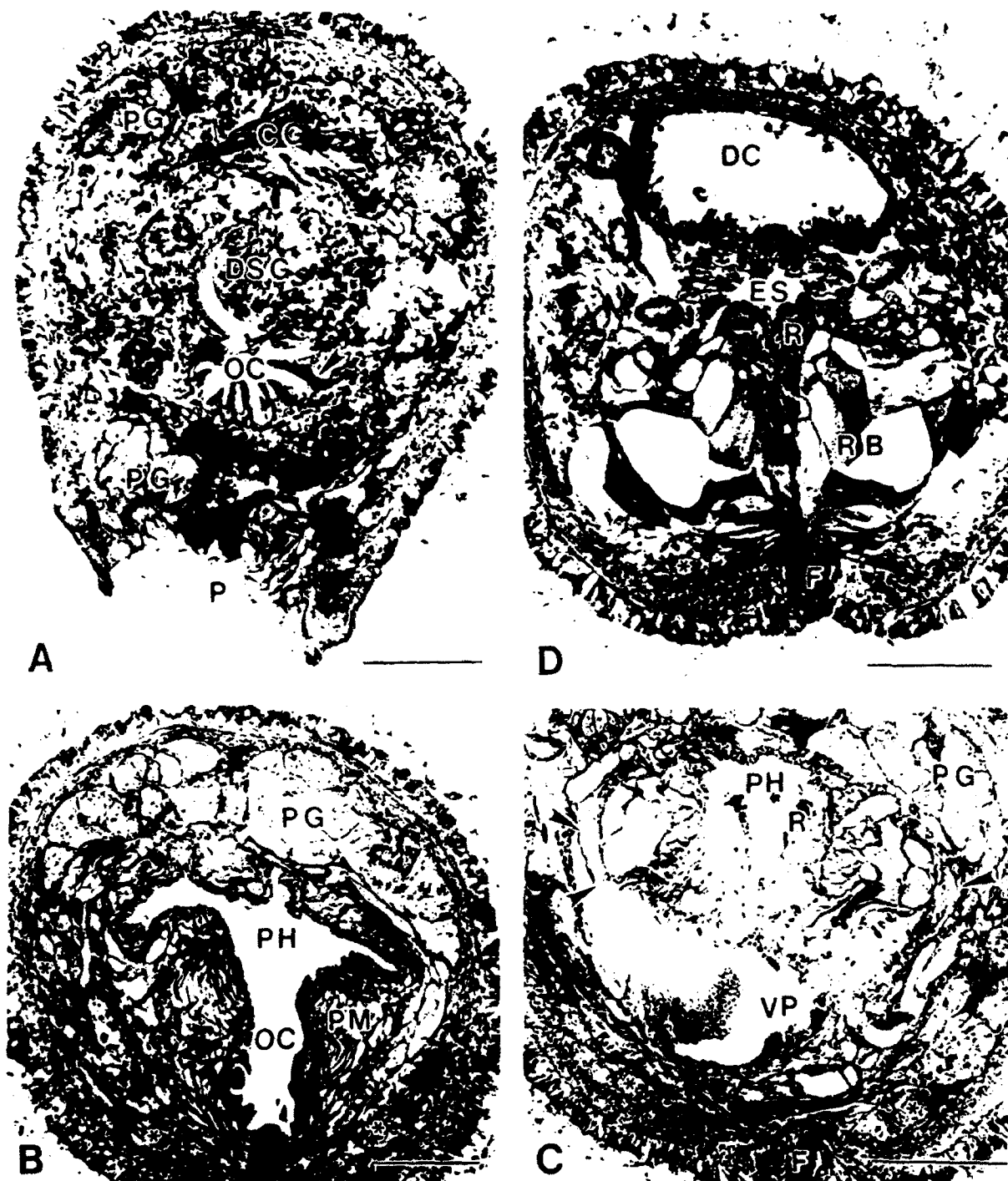
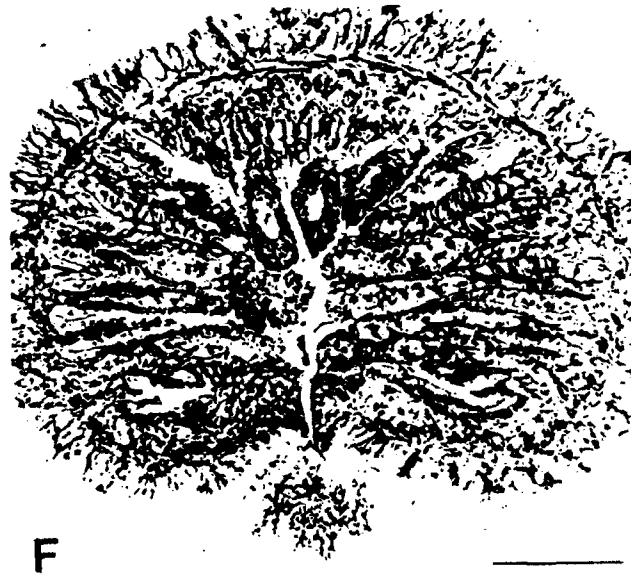
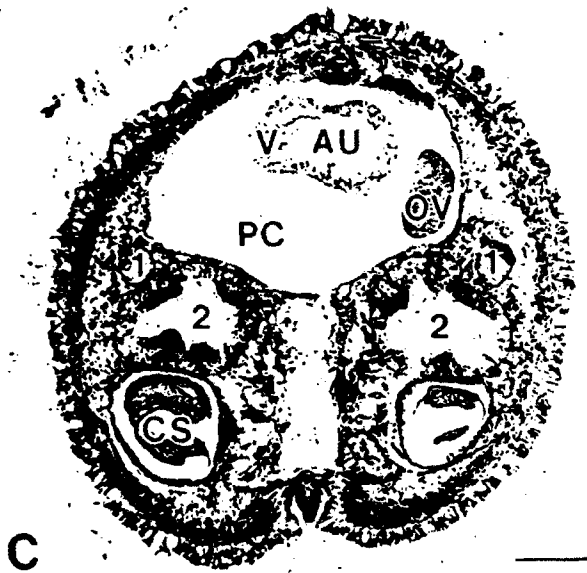
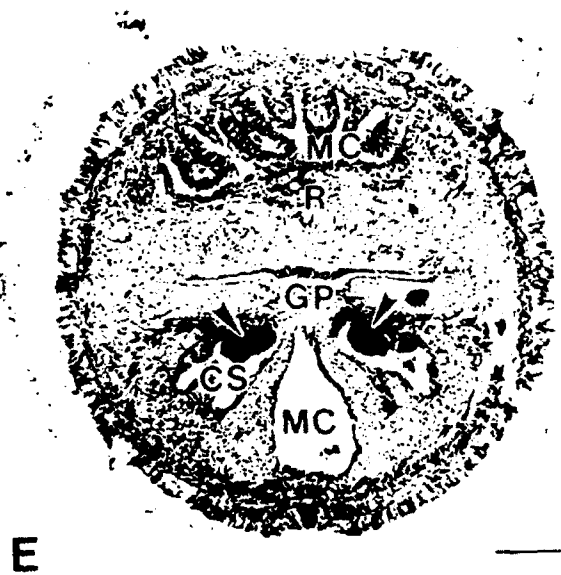
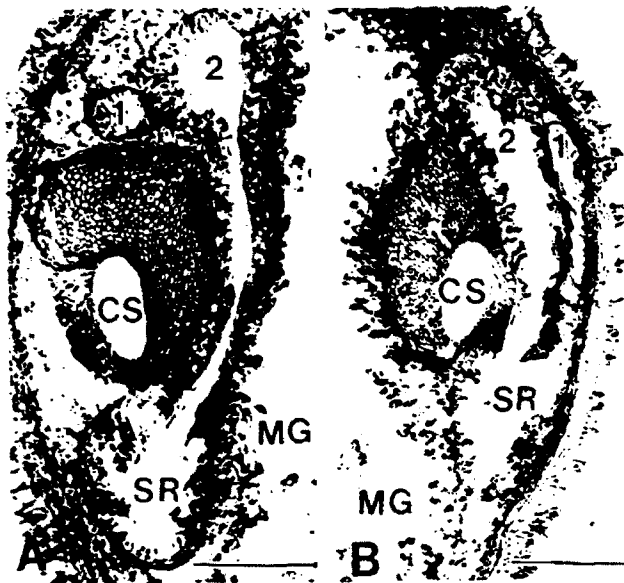


Figure 4

Anterior end, *Helicoradomenia juani*, transverse histologic sections 1 through 4 of Figure 1D. A: Section 1 through cerebral ganglion, dorsal salivary gland, oral cavity with cirri (arrowhead), and pedal pit. B: Section 2 through oral cavity, pharynx, and pharyngeal muscles. C: Section 3 through paired ventral salivary glands (arrowheads), gland on left shown opening into anteroventral radular pocket. D: Section 4 through dorsal cecum of midgut, esophagus, radula and radula bolster with well-developed musculature and large chondroid-like cells. Key. CG, cerebral ganglion; DC, dorsal cecum; DSG, dorsal salivary gland; ES, esophagus; F, foot; OC, oral cavity; P, pedal pit; PG, pedal gland; PH, pharynx; PM, pharyngeal muscle; R, radula; RB, radula bolster; VP, anteroventral radular pocket. Asterisks indicate ganglia of lateral and anteroventral nerve cords. Scale bars: A-D = 0.1 mm.



latter five genera are drawn from sectioned material only, they all appear to be distichous denticulate bars.

SALVINI-PLAWEN (1978) placed the family Simrothiellidae in the order Cavibelonia, a grouping based on possession of hollow spicules. *Helicoradomenia* is the second genus with solid spicules to be placed in a cavibelonid family. The genera of Pararrhopalidae, if brought together on the basis of possessing fishhook-shaped spicules, also form a cavibelonid family with both solid (*Ocheyoherpia*) and hollow spicules (SCHELTEMA, in press). The families of Cavibelonia vary in respect to type of radula and ventral salivary glands and in presence or absence of skeletal spicules (SALVINI-PLAWEN, 1985). The morphologies of these structures are not unique to the Cavibelonia but are found in other orders as well. We therefore conclude that the order Cavibelonia is polyphyletic and needs to be revised. The family Simrothiellidae should probably be raised to ordinal level, but not until further comparisons of newly collected material have been made.

**Distribution:** Several vent species of *Helicoradomenia* still to be described occur at other rift sites in the eastern Pacific other than those off the northwest United States where *H. juani* is found: off the Galápagos (2 species), at 13°N (1 species), at 20°N (3 species, one in common with Galápagos), and from Gorda Ridge (1 species). The genus has also been collected from western Pacific rift sites in the Marianas Back Arc and Lau basins. None of these species has been collected in such high numbers as *H. juani*.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- GEGENBAUR, C. 1878. Grundriss der Vergleichenden Anatomie, 2nd ed. Wilhelm Engelmann: Leipzig.
- KOREN, G. & D. C. DANIELSSON. 1877. Beskrivelse over nye arter, henhørende til slægten Solenopus, samt nogle oplysninger om dens organisation. Archiv for matematik og Naturvidenskab 2:120-128.
- NIERSTRASZ, H. F. 1902. The Solenogastres of the Siboga-Expedition. Siboga-Expedition 47. E. J. Brill: Leyden. 46 pp.
- NIERSTRASZ, H. F. 1903a. *Kruppomenia minima* n.g. n.sp., p. 249, pl. 7, fig. 5. In: S. Lo Bianco, Le pesche abissali del Mediterraneo. Mittheilungen aus der Zoologischen Station zu Neapel 16:109-278.
- NIERSTRASZ, H. F. 1903b. Neue Solenogastren. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Thiere 18:359-386.
- PELSENEER, P. 1906. A treatise on zoology. In: E. R. Lankester (ed.), Part 5, Mollusca. Black: London.
- PILSBRY, H. A. 1898. Order Aplacophora v. Ihering. Tryon's Manual of Conchology 17:281-310.
- SALVINI-PLAWEN, L. v. 1967. Neue Scandinavische Aplacophora (Mollusca, Aculifera). Sarsia 27:1-63.
- SALVINI-PLAWEN, L. v. 1968. Neue Formen im marinen Mesopsammon: Kamptozoa und Aculifera (nebst der für Adria neuen Sandfauna). Annalen des Naturhistorischen Museums in Wien 72:231-272.
- SALVINI-PLAWEN, L. v. 1978. Antarktische und subantarktische Solenogastres (eine Monographie: 1898-1984). Zoologica (Stuttgart) 44:1-315.
- SALVINI-PLAWEN, L. v. 1985. Early evolution and the primitive groups. Pp. 59-150. In: E. R. Trueman & M. R. Clarke (eds.), The Mollusca. Vol. 10. Evolution. Academic Press, Inc.: Orlando.
- SCHELTEMA, A. H. 1988. Ancestors and descendants: relationships of the Aplacophora and Polyplacophora. American Malacological Bulletin 6:57-68.
- SCHELTEMA, A. H. In press. Class Aplacophora. In: D. Walton & P. Beesley (eds.), Fauna of Australia. Vol. 5. Mollusca. Australian Biological Resources Study, Canberra.
- TURNER, R. D. 1985. Notes on the mollusks of deep-sea vents and reducing sediments. American Malacological Bulletin Special Edition 1:23-34.

Figure 5

Posterior end, *Helicoradomenia juani*, transverse histologic sections 5 through 8 of Figure 1D. A, B: Section 5, left and right sides, respectively, showing the connections between the upper and lower gametoducts and the paired seminal receptacles; position of ducts on left side lies between copulatory spicules and midgut, whereas those on right lie lateral to the copulatory spicules. C: Section 6 through pericardium with ovum, heart, upper and lower gametoducts, and copulatory spicule pockets. D: Section 7 through posterior end of pericardial cavity where it connects to upper gametoduct, beginning of auricle, rectum and suprarectal commissure arising from large ganglion of the lateral nerve cord (asterisk). E: Unnumbered section between sections 7 and 8 through proximal end of mantle cavity just anterior to openings of rectum and gametopore and through the copulatory spicule glands (arrowheads). F: Section 8 through mantle cavity with long respiratory papillae. G: Unnumbered section posterior to F through the accessory copulatory spicules (dissolved) of the mantle, bump indicated by arrowhead (cf. Figure 3C). Key: 1, upper gametoduct; 2, lower gametoduct; AS, accessory copulatory spicule; AU, auricle; CS, copulatory spicule/spicule pocket; GP, gametopore; MC, mantle cavity; MG, midgut gland; OV, ovum; PC, pericardial cavity; R, rectum; SC, suprarectal commissure; SR, seminal receptacle; V, ventricle. Scale bars: A-C, E, F = 0.1 mm; D, G = 0.05 mm.



# *Chaetoderma argenteum* Heath, a Northeastern Pacific Aplacophoran Mollusk Redescribed (Chaetodermomorpha: Chaetodermatidae)

by

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**Abstract** *Chaetoderma argenteum* Heath, 1911, has been collected in the northeast Pacific from Point Conception, California, to southeast Alaska between 70 and 600 m. Synonyms are *C. attenuata* Heath, 1911, and *C. montereyensis* Heath, 1911. Since 1960, several surveys have taken *C. argenteum* from the Santa Maria Basin, from off the Oregon coast, and from both offshore and inshore waters of southwest British Columbia in numbers large enough to provide material for experimental research.

*Chaetoderma argenteum* is redescribed and illustrated. It is distinguished from all other *Chaetoderma* species of the east Pacific by the anterior trunk spicules, which are bent and thickened on each side of an abfrontal groove, and by the large radula cone, which is curved in lateral view.

## INTRODUCTION

*Chaetoderma argenteum* Heath, 1911, can predictably be collected from off southwestern Vancouver Island, British Columbia, from fine silt sediments, between 100 and 200 m. Specimens from this locality provided material for the first published account of spermiogenesis in a chaetoderm aplacophoran (BUCKLAND-NICKS & CHIA, 1989). The species has also recently been collected from inshore waters of British Columbia, from off the Oregon coast, and from the Santa Maria Basin off southern California. It thus appears to occur in large enough numbers at specific localities to provide material for fine structural analysis of anatomy and larval development, both of which are poorly studied in this group.

HEATH's (1911) original descriptions are not adequate for accurate species identification; he even mistook different sizes of *Chaetoderma argenteum* for different species.

Therefore this species is redescribed by external anatomy and morphology of hard parts using the criteria of SCHELTEMA (1976, 1989).

## MATERIALS AND METHODS

Two hundred eleven specimens have been examined, 13 certain holotype and paratype specimens and 16 presumed paratypes collected between 1903 and 1904 by the U.S. Fisheries steamer *Albatross* (Table 1) and 172 recently collected specimens (Table 2). Most of the recently collected specimens were fixed as part of entire quantitative grab samples and sorted post-fixation. The fixatives used were not known to the authors; preservation was in buffered alcohol. Specimens used for scanning electron microscopy (SEM) were sorted alive, dissected, and then fixed in 2% glutaraldehyde buffered with 0.2 M sodium cacodylate.





Table 1  
*Chaetoderma argenteum* Heath, 1911, extant type material re-examined.

Albatross <sup>1</sup> station	Locality	Depth (m)	Date (day/mo/yr)	No. specimens		Source <sup>2</sup>
				Listed by Heath	Extant	
4231	Naha Bay, SE Alaska	148-203	7/VII/03	1	1, slides <sup>3</sup>	CAS
4244	Kasaan Bay, SE Alaska	90-97	11/VII/03	1	—	—
4244, 4250	Samples mixed	—	—	—	3	MCZ
4250	off Stikine R., SE Alaska	110-119	13/VII/03	5	1	MCZ
					1, slides <sup>3</sup>	CAS
4252	Stephens Passage, SE Alaska	356-362	14/VII/03	2	2	MCZ
4485	Monterey Bay	70-194	17/V/04	9	—	—
4508	Monterey Bay	526-640	20/V/04	7	—	—
4510 <sup>4</sup>	Monterey Bay	164-331	?/V/04	—	19	MCZ
4522	Monterey Bay	234-268	26/V/04	139	1	MCZ
4523	Monterey Bay	135-194	26/V/04		1	MCZ
4524	Monterey Bay	383-410	26/V/04		2	MCZ
4525	Monterey Bay	400	26/V/04		—	—
4526 <sup>4</sup>	Monterey Bay	367	26/V/04	—	7	MCZ
n.d.	Monterey Bay	n.d.	n.d.	1	1, slides <sup>3</sup>	CAS

<sup>1</sup> From U.S. COMMISSION OF FISH AND FISHERIES (1905) and U.S. BUREAU OF FISHERIES (1906).

<sup>2</sup> CAS = California Academy of Sciences; MCZ = Museum of Comparative Zoology (Harvard University).

<sup>3</sup> Holotypes.

<sup>4</sup> Not listed by HEATH (1911) but specimens were presumably examined by him and are considered to be paratypes.

dylate buffer (pH 7.4) at 4°C for 2 h. Following a rinse in the same buffer, tissues were post-fixed in 1% osmium tetroxide in the same buffer at 4°C for 1 h. The tissues were dehydrated in an ethanol series, exchanged in incremental steps through amyl acetate, and critical point dried. Selected body parts were mounted on SEM stubs, sputter coated with gold, and examined in a Cambridge S250 stereoscan scanning electron microscope.

Spicules used for camera lucida drawings were removed from alcohol-preserved specimens with a fine needle and transferred by pipette into glycerine; or the specimen was placed directly into glycerine before removing the spicules. For SEM, segments of specific areas were isolated and treated with 2% sodium hypochlorite (household bleach) until the tissues were dissolved. Spicules were removed from the dish with a Pasteur pipette, passed

through three rinses of distilled water, transferred into ethanol, and then air dried on SEM stubs. The spicules were sputter coated with gold prior to examination. Radulae for camera lucida drawings were dissected by making a dorsal longitudinal slit in the head region, removing the entire buccal mass, and dissolving the tissue in hypochlorite solution. The radulae were washed thoroughly and placed in glycerine for drawing. Preparation of radulae for SEM was similar to that for spicules.

Body measurements of entire preserved specimens were made from camera lucida drawings with dividers or a map-measuring wheel, and of sectioned type material with scale bars drawn on camera lucida drawings.

Type material is at the California Academy of Sciences (CAS) and Museum of Comparative Zoology (Harvard University) (MCZ).

Table 2  
*Chaetoderma argenteum* Heath examined from recent collections.

Locality	Depth (m)	No. specimens	Source <sup>1</sup>
Off SW Vancouver Is., BC	100-200	96	SEATECH-IOS; Buckland-Nicks
Alice Arm, Hastings Arm, of Observatory Inlet, BC	400-600	36	IOS
Saanich Inlet, BC	90	4 <sup>2</sup>	D. A. Bright, Univ. Victoria
Off Oregon coast	150-200	11	OSU
Santa Maria Basin	113-410	25 <sup>2</sup>	MMS; Santa Barbara Museum

<sup>1</sup> SEATECH-IOS = Canadian Government Survey, Institute of Ocean Sciences, Sidney, BC; OSU = Oregon State University; MMS = Minerals Management Service, U.S. Department of Interior.

<sup>2</sup> Voucher specimens only.

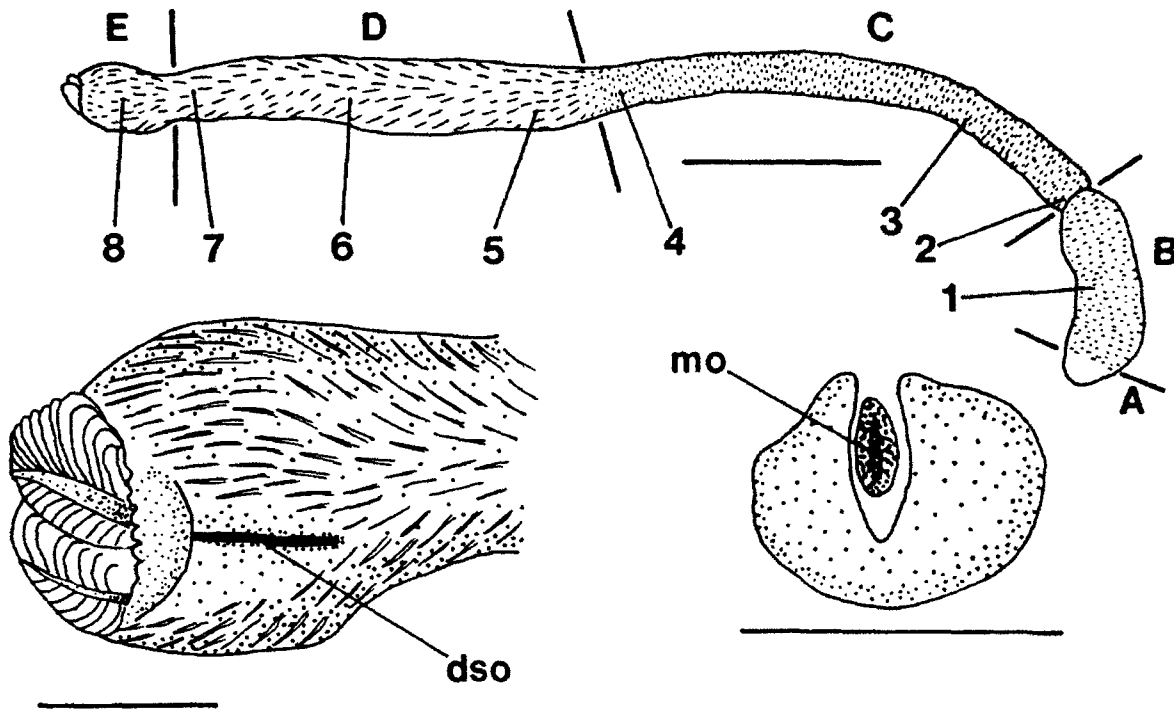


Figure 1

*Chaetoderma argenteum* Heath. *Chaetoderma montereyensis* Heath paratype (Albatross stn. 4524) (MCZ). Above, entire specimen showing body regions: A, anterium; B, neck; C, anterior trunk; D, posterior trunk; E, posteriorium; and positions 1-8 from which spicules were drawn (see Figure 3); scale bar = 5.0 mm. Lower left, posteriorium showing extended ctenidia (cf. Figure 2C) and dorsoterminal sense organ (dso); lower right, oral shield with dorsal cleft around mouth opening (mo) (cf. Figure 2D). Lower left and right, same paratype as above; scale bars = 1.0 mm.

## SYSTEMATICS

### Subclass Chaetodermomorpha Pelseneer, 1906

#### Caudofoveata Boettger, 1956

Aplacophoran mollusks without a foot or ventral groove; with a cuticular oral shield and paired ctenidia in the mantle cavity; stomach and digestive gland separate; dioecious.

#### Family CHAETODERMATIDAE Marion, 1885

Oral shield unpaired; radula with a cone-shaped cuticular piece (=peg, tongue) and a single pair of denticles; body with four distinct regions reflecting internal anatomy.

#### *Chaetoderma* Lovén, 1844

*Crystallophrisson* Möbius, 1875. IVANOV, 1981 (see SALVINI-PLAWEN, 1984).

**Type species:** *Chaetoderma nitidulum* Lovén, 1844, by monotypy.

Radula with paired denticles lying outside dome-shaped cuticular membrane that covers buccal mass and with paired lateral projections extending from radula cone to dome-

shaped membrane beneath base of denticles (see SCHELTENA, 1972).

**Range:** Worldwide from 8 to 2260 m.

#### *Chaetoderma argenteum* Heath, 1911

*Chaetoderma argenteum* HEATH, 1911:43, 62-63, pl. 4 fig. 7, pl. 26 figs. 1-7, pl. 36 fig. 1, pl. 37 fig. 6 (SE Alaska, Behm Canal, near Naha Bay, 148-203 m; Albatross stn. 4231, 7/VII/03. **Type:** Holotype as serial sections and spicules, CAS 021392. Described from single specimen.

*Chaetoderma attenuata* HEATH, 1911:43, 55-59, pl. 4 figs. 3, 10, pl. 5 fig. 1, pl. 12 fig. 4, pl. 25 figs. 1-10 [figs. 1-3, 6, 7 of type], pl. 36 fig. 2, pl. 37 fig. 8 (SE Alaska, Stikine River delta, 110-119 m; Albatross stn. 4250, 13/VII/03). **Types:** Holotype as serial sections and spicules, CAS 021393; paratypes as 6 wet specimens, MCZ.

*Chaetoderma montereyensis* HEATH, 1911:43, 61-62, pl. 4 figs. 4, 8, 14, 17, pl. 27 figs. 1, 2, 4-11 [figs. 2, 5, 7-9 of type], pl. 37 figs. 2, 3 (Monterey Bay, California) (no Albatross stn. no.). **Types:** Holotype as serial sections, no spicule slide, CAS 021397; 4 certain and 26 probable paratypes as wet specimens, MCZ.

?*Crystallophrisson kabanovi* IVANOV, 1984. [Caudofoveata (Mollusca, Caudofoveata) in Peter the Great Bay (Sea of Japan)] pp. 36-37, fig. 4. [In Russian.]

*Chaetoderma* sp. BUCKLAND-NICKS & CHIA, 1989:308-317, figs. 1-22.

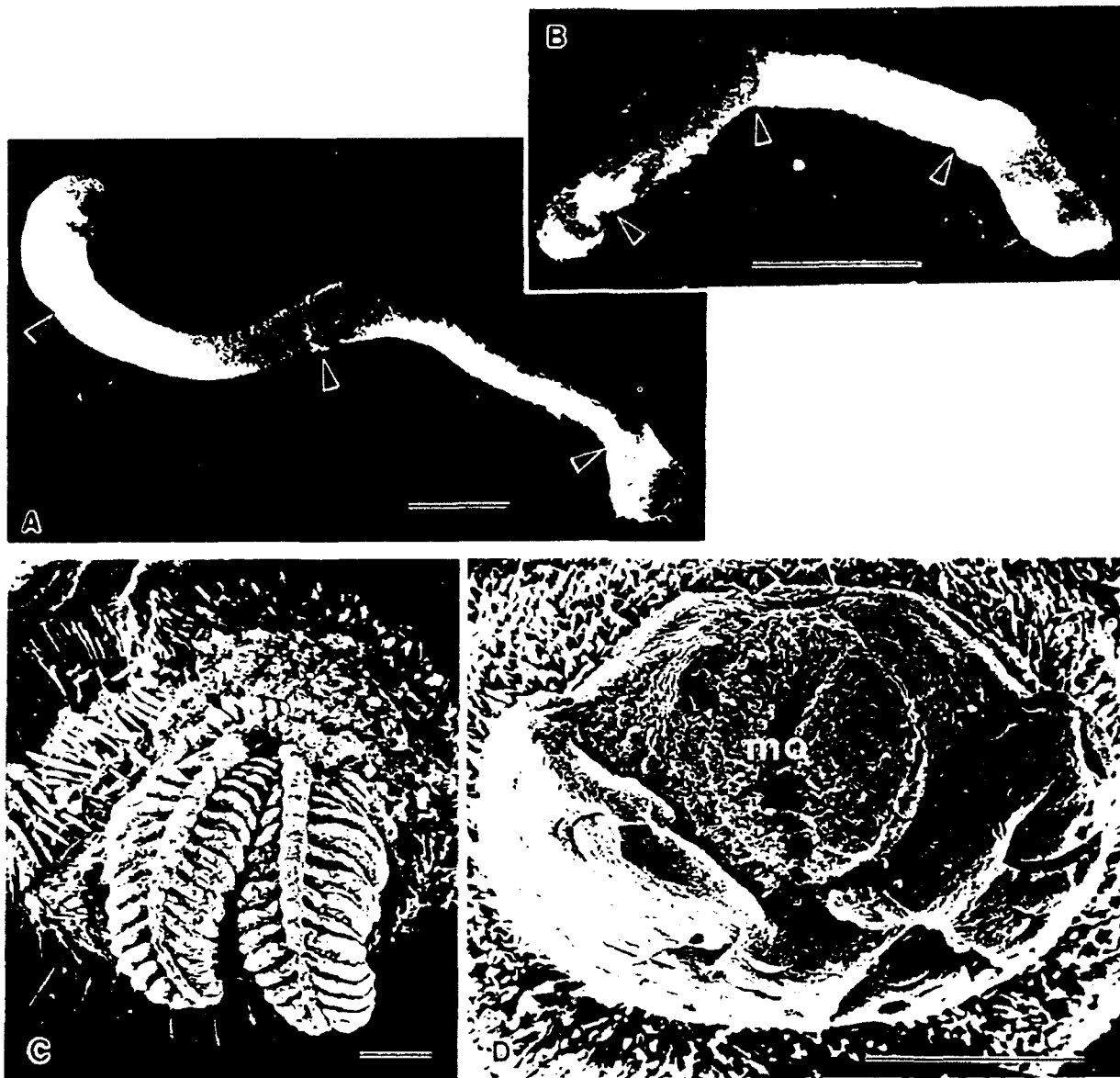


Figure 2

*Chaetoderma argenteum* Heath from 110 m adjacent to Rainy Bay, Vancouver Island, BC: A, B. Living specimens showing change in shape caused by muscle contraction and hydrostatic expansion. Arrowheads indicate boundaries between body regions (cf. Figure 1). C: Ctenidia extended from mantle cavity, scanning electron photomicrograph (SEM); long axes indicate dorsally situated efferent channels, and ctenidial leaves are alternate. D: Oral shield with open mouth (mo); arrowheads indicate edge of cuticle at dorsal cleft. Note that ventral part of shield appears thicker than dorsal part around mouth. Scale bars: A, B = 3 mm, C, D = 200  $\mu$ m.

**Range:** Off Pt. Conception, California, to southeast Alaska, from 70 to 640 m; ?Sea of Japan, 33–69 m

**Diagnosis:** Greatest length to more than 40 mm, anterior constriction pronounced; anterior trunk usually longer than posterior trunk and often narrower than neck, posterior trunk up to 2.0 mm in diameter. Oral shield with dorsal cleft. Spicules erect on anterior trunk and flat against posterior trunk. Spicules widest at base, those of anterior trunk bent, thickened on each side of base forming abfrontal

groove, up to 130  $\mu$ m long, those of posterior trunk pyramidal, flat, keeled, with two or more sharp lateral ridges, up to 263  $\mu$ m, radula cone large, up to 510  $\mu$ m long, curved, wider laterally than frontally, lateral projections up to 250  $\mu$ m long

#### DESCRIPTION

**Body:** Preserved, contracted specimens of *Chaetoderma argenteum* typically have an anterior trunk region (C) either

Table 3

Body measurements and ratios of specimens belonging to Heath types of *Chaetoderma argenteum*, *C. attenuata*, and *C. montereyensis*.

Species	Measurements (mm)											
	Body length			Neck (B) diam. <sup>1</sup>			Ant. trunk (C) diam. <sup>1</sup>			Post. trunk (D) diam. <sup>1</sup>		
	ar.	at.	m.	ar.	at.	m.	ar.	at.	m.	ar.	at.	m.
Heath, 1911 <sup>2</sup>	24	45, 61	45	—	—	—	1.6	1.5, 1.7	2	2.6	2.6, 2.7	3
Type slides	—	—	—	1.2	—	—	0.8	0.5	1.3	1.1	0.8	1.4
Paratypes <sup>3</sup>	—	39-42	14-34	—	1.0-1.6	0.8-1.5	—	0.8-1.2	0.8-1.4	—	1.1-1.9	0.8-2.0

	Ratios								
	B/C diam.			C/D length			C/D diam.		
	ar.	at.	m.	ar.	at.	m.	ar.	at.	m.
Computed from Heath, 1911	—	—	—	—	—	—	0.62	0.65	0.67
Type slides	1.50	—	—	1.46 <sup>4</sup>	—	—	0.72	0.62	0.93
Paratypes <sup>3</sup> (mean)	—	1.26	1.05	—	1.45	1.10	—	0.64	0.80

<sup>1</sup> See Figure 1 for body regions.

<sup>2</sup> Heath does not state whether these are measurements of alive or fixed animals.

<sup>3</sup> For *C. montereyensis*, all *Albatross* specimens are considered to be paratypes.

<sup>4</sup> Determined from pl. 4, fig. 7 (HEATH, 1911).

equal in diameter to or narrower than the neck (region B) and longer than the posterior trunk (region D) (Figure 1, Table 3). In living specimens the relative lengths of the two trunk regions change, reflecting movements under hydrostatic control (cf. Figure 2A, B). The erect spicules of the neck and anterior trunk are dense; the flat-lying spicules of the posterior trunk are more sparse. The oral shield is cleft dorsally (Figures 1, 2), a morphology that was recognized by HEATH (1911) in *C. attenuata*, but that he illustrated incorrectly in *C. montereyensis* as being pierced by the mouth opening (HEATH, 1911: pl. 4, figs. 14, 17). Posteriorly the dorsoterminal sense organ is obvious and about 1 mm in length in large specimens. The spicules of the posterium do not form a terminal ring.

**Spicules:** Spicules from all body regions are widest basally and range up to more than 10  $\mu$ m in thickness. Neck spicules (no. 1, Figures 3, 5) are mostly narrow, thickest medially at the flared base, and curved in lateral view; they are less than 100  $\mu$ m long and up to 25  $\mu$ m wide. Spicules from the anterior trunk are longest near the anterior constriction (no. 2), up to 130  $\mu$ m in length, decreasing to 90  $\mu$ m at the midpoint (no. 3) and to 80  $\mu$ m next to the posterior trunk (no. 4). All are thickened on each side abfrontally producing a groove (Figures 3, isochromes; 5E) and all are bent and flared basally, ranging up to 40  $\mu$ m wide. Spicules near the posterior trunk bear a sharp keel (no. 4). Spicules on the posterior trunk region change abruptly; they are flat, sharply keeled with one or more sharp or rounded lateral ridges on each side, and gradually tapered from the broad base (nos. 5-7). Length increases from a maximum of 170  $\mu$ m anteriorly to 265  $\mu$ m posteriorly and greatest width at the base increases

from 50 to 60  $\mu$ m. Thickness exceeds 10  $\mu$ m only medially on the keel. There are numerous fine axial striations on the base (Figure 5C). Spicules of the posterium are without a keel, more than 400  $\mu$ m long, 40  $\mu$ m or more wide, and thickest medially (no. 8).

**Radula:** The cone-shaped piece is large, up to 510  $\mu$ m long, 140  $\mu$ m wide in frontal view, and 190  $\mu$ m wide in lateral view (Figures 4, 5); in lateral view it curves and tapers to a narrow end. The lateral projections are broad and up to 250  $\mu$ m long. Denticles are rather small, between 30 and 60  $\mu$ m long. The cuticular dome extends proximally one-half the length of the cone. (Measurements based on five isolated redulae.)

## REMARKS

Heath considered *Chaetoderma argenteum* of different sizes or from geographically separated populations as distinct species, although he did not differentiate *C. argenteum*, *C. attenuata*, and *C. montereyensis* either by written description or by illustration. STORK (1941) already noted the similarity between *C. attenuata* and *C. montereyensis* in Heath's descriptions. In several characters examined here in types and newly collected specimens, no differences at a species level were detected among the three *Chaetoderma* species described by Heath. Precedence is given to the name *C. argenteum* because of its page position (HEATH, 1911: 43).

The lengths and diameters of body regions and their ratios are shown in Table 3 for Heath's types and paratypes. Although total body length as published by Heath and measured on types is seen to differ among his species,

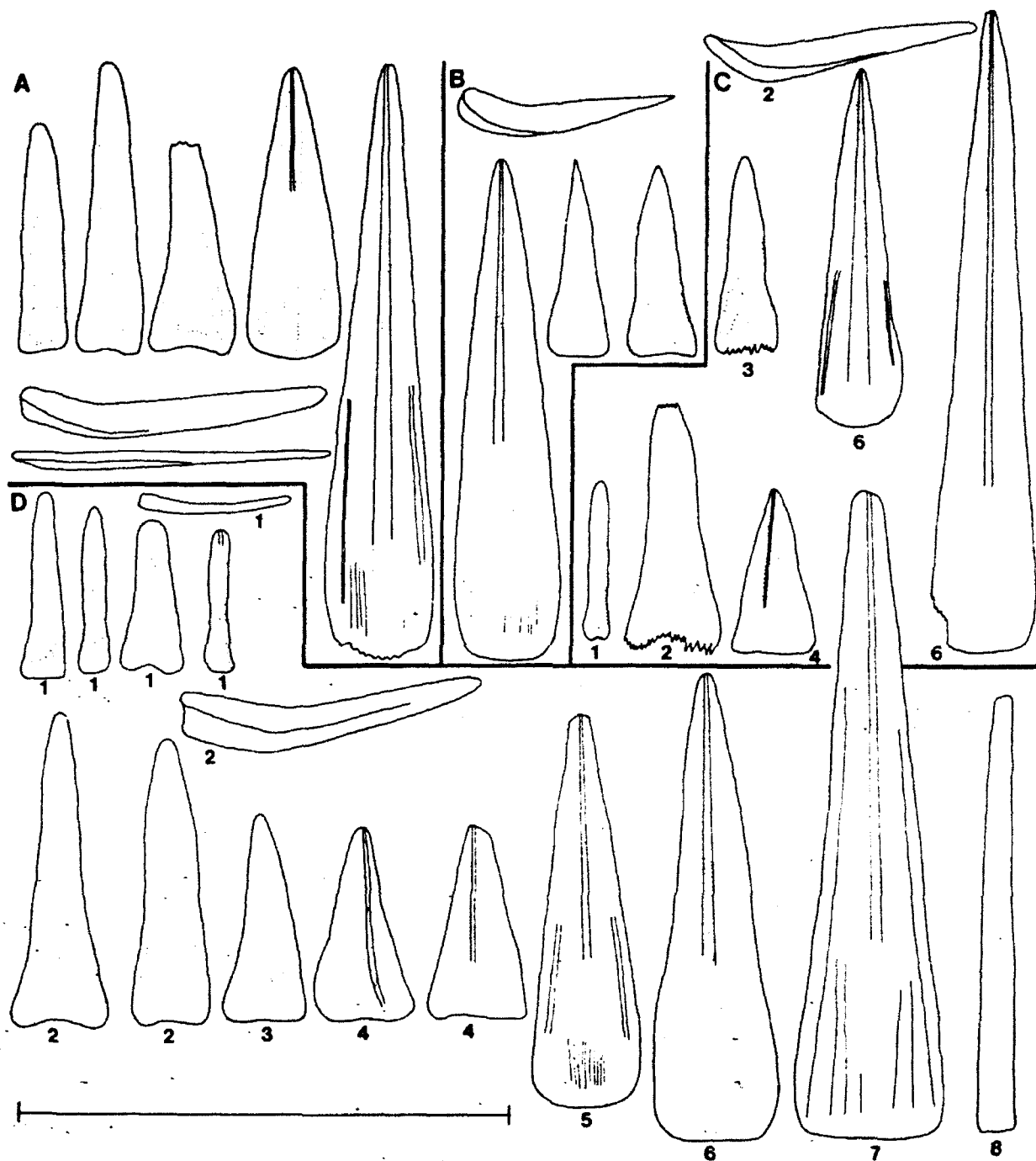


Figure 3

Spicules of *Chaetoderma argenteum* Heath. Lateral views with long axis horizontal; isochromes (lines of equal thickness as seen under cross-polarized light) indicated by dotted lines. A: Holotype spicules, *C. argenteum*, CAS 021392. B: Holotype spicules, *C. attenuata* Heath, CAS 021393. C: Paratype spicules, *C. attenuata* (Albatross str. 4252, MCZ); numbers refer to body positions indicated in Figure 1. D: Paratype spicules, *C. montereyensis*, from specimen drawn in Figure 1 showing positions 1-8 from which spicules were drawn. Scale bar = 200  $\mu\text{m}$ , except for spicule D8 = 500  $\mu\text{m}$ .

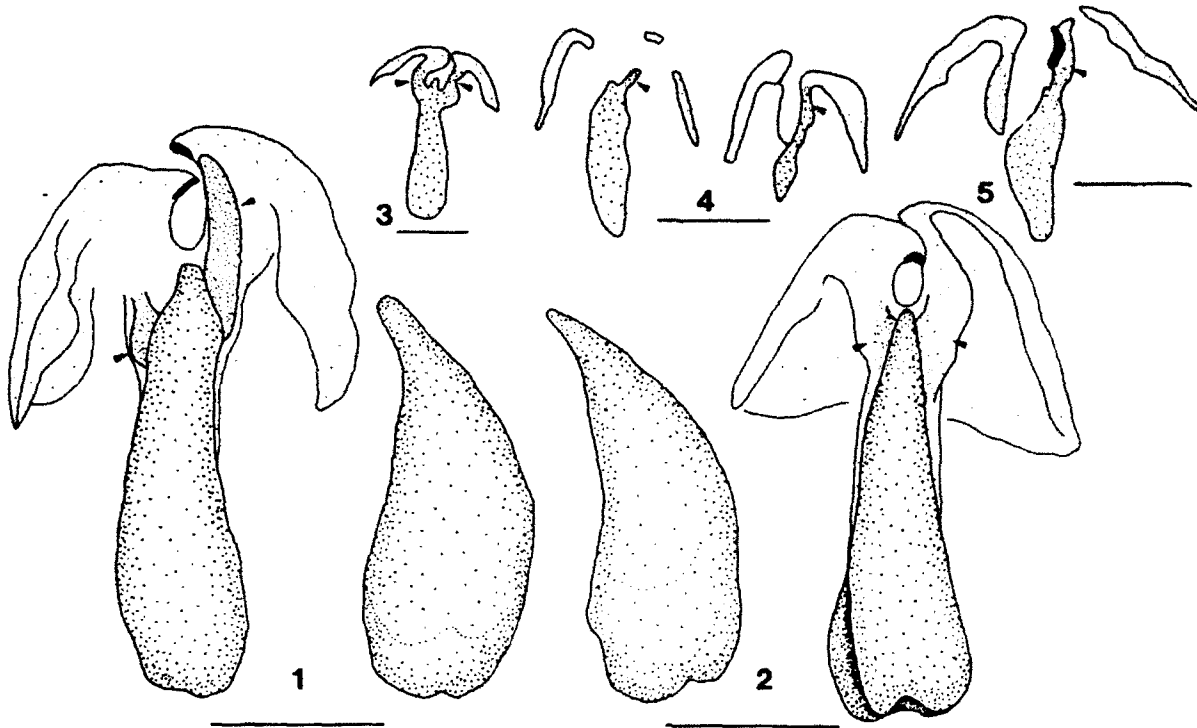


Figure 4

Radula of *Chaetoderma argenteum* Heath (cf. Figure 5C, D). 1: Frontal and lateral views of *C. attenuata* Heath paratype (MCZ) (Albatross stn. 4252). 2: Lateral and frontal views of *C. montereyensis* Heath, specimen presumed part of type series (MCZ) (Albatross stn. 4510). 3: Section of *C. attenuata* Heath holotype (CAS 021393). 4: Two sections of *C. argenteum* Heath holotype (CAS 021392). 5: Section of *C. montereyensis* Heath holotype (CAS 021397). Arrowheads indicate lateral projections. Scale bars = 200  $\mu$ m.

measured diameters of the neck (region B), anterior trunk (region C), and posterior trunk (region D) fall within the same ranges (0.8–1.6 mm, 0.5–1.4 mm, and 0.8–2.0 mm, respectively). The ratios of neck to anterior trunk diameters, anterior to posterior trunk diameters, and anterior to posterior trunk lengths are also similar. In particular, the neck is usually wider than the anterior trunk (ratios 1.50, 1.26, and 1.05 for Heath's three species) and the anterior trunk is longer on average than the posterior trunk (ratios 1.46, 1.45, and 1.10).

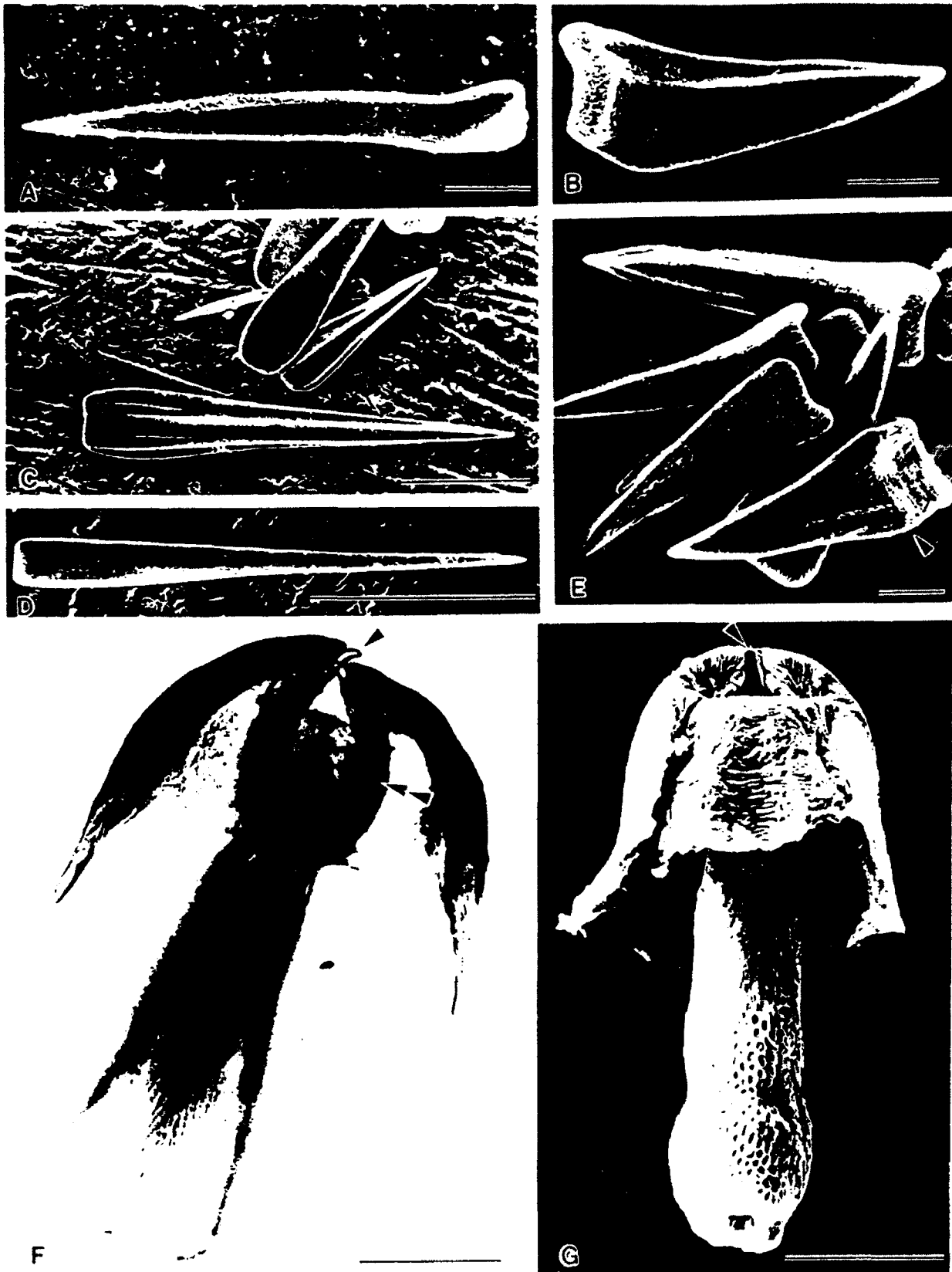
The oral shield is unknown for the single specimen of *Chaetoderma argenteum* described by Heath, but shields of paratypes of *C. attenuata* and *C. montereyensis* do not differ either in size or in being dorsally cleft, despite HEATH's

qualitative judgments of differences in relative size (1911: 43) or incorrect illustrations (1911: pl. 4, figs. 14, 17).

Heath fortunately made permanent spicule slides from the holotypes of *Chaetoderma argenteum* and *C. attenuata*. Paratypes of *C. montereyensis* and *C. attenuata* remained in good condition after nearly 90 years in alcohol and provided spicules from discrete body regions (Figures 1, 3). All of Heath's species have the diagnostic short, bent spicules with a broadly flared base and lateral abfrontal thickenings. These spicules are carried erect on the anterior trunk of *C. attenuata* and *C. montereyensis* paratypes. The same spicule attitude is indicated in the sections of the *C. argenteum* holotype, where the arrangement of spaces left by dissolved spicules in the cuticle of the anterior trunk

Figure 5

*Chaetoderma argenteum* Heath: spicules (A–E, scanning electron micrographs, cf. Figure 3) and radulae (F, light microscope, G, SEM, cf. Figure 4) from specimens recently collected off Rainy Bay, BC. A: From neck region. B, E: From anterior trunk; arrowhead on E indicates abfrontal view of broad lateral ridges and groove. C: From posterior trunk. D: From posterior. F: Frontal view, lateral projections (double arrowhead) and denticles (single arrowhead) seen in transmitted light. Note that cone becomes progressively tapered distally. G: Dome-shaped cuticular hood covering buccal mass as seen with SEM; denticles (arrowhead) lie outside of cuticular dome. Scale bars: A, B, E = 20  $\mu$ m; C, D, F, G = 100  $\mu$ m.



are the same as the spicule spaces in *C. attenuata* and *C. montereyensis* holotype sections from the same body region. The morphology of spicules from the anterior trunk separates *C. argenteum* from all other eastern Pacific *Chaetoderma* species.

The radulae from paratypes of *Chaetoderma attenuata* and *C. montereyensis* are morphologically indistinguishable. The cone is wide and curved in lateral view and the lateral projections are long and broad (Figure 4). The radula is broken in the holotype sections of *C. argenteum*, but size of the radula in relation to section diameter and size of the lateral projections are similar to those in holotype sections of *C. attenuata* and *C. montereyensis* (Figure 4, radulae 3, 4, 5).

A comparison of HEATH's (1911) written descriptions and examination of type sections of *Chaetoderma argenteum*, *C. attenuata*, and *C. montereyensis* offer no specific differences. Finally, new collections of Aplacophora from areas close to the type localities of *C. argenteum* and *C. attenuata* contain only a single species with bent, laterally thickened anterior trunk spicules. Therefore, we can conclude with a high degree of certainty that the synonymy is justified.

### GEOGRAPHIC DISTRIBUTION

Including *Chaetoderma argenteum* and its synonyms, HEATH (1911) named eight northeast Pacific *Chaetoderma* species from Albatross collections. SCHWABL (1963) added nine further species from southern California collected during the Pacific Expedition of the Allan Hancock Foundation. Examination of Schwabl and Heath types indicates a reduction of these species by synonymy to perhaps 10 species, including *C. argenteum*. The number of *Chaetoderma* species known worldwide is about 37 to date; thus, approximately one-quarter of known species occurs in the northeast Pacific. The genus ranges in depth from 8 to 2260 m, but only a few species are restricted to depths less than 100 m or extend to more than 1000 m. The northeast Pacific species fit this depth pattern and are thus members of the upper continental slope fauna.

*Chaetoderma argenteum* has an amphi-Pacific distribution if *Crystallophrisson kafanovi* Ivanov (= *Chaetoderma kafanovi*) from the Sea of Japan is a synonym. There is at least one other probable amphi-oceanic *Chaetoderma* species. In the northern Atlantic, *C. nitidulum*, known as *C. nitidulum canadense* Nierstrasz in the western Atlantic (SCHELTEMA, 1973) (but considered a distinct species by SALVINI-PLAWEN, 1978), seems to occur on both sides of the ocean.

In 1904 numerous specimens of *Chaetoderma argenteum* were taken by the Albatross in Monterey Bay (Table 1), but since then it has been replaced by another unidentified species probably related to a form found south of Pt. Conception. However, *C. argenteum* has recently been collected south of Monterey Bay in the Santa Maria Basin from 113 to 410 m (Table 2).

### ENVIRONMENT

In two studies of the effects of mine tailings on density and distribution of the invertebrate fauna in the inner reaches of Observatory Inlet, British Columbia (KATHMAN *et al.*, 1983, 1984), *Chaetoderma argenteum* was too scarce to be used as an indicator species. The study did show that the species was most abundant (50 m<sup>-2</sup>) in sediments of fine silt and clay near the sill at depths between 400 and 600 m, an area physically, chemically, and biologically different from the inner reaches. Adjacent to Rainy Bay, near Bamfield, Vancouver Island, British Columbia, *Chaetoderma argenteum* has repeatedly been found in similar fine silts at 110 m. It seems that the most likely sites for finding *C. argenteum* are the fjords and inlets of Canada and southeast Alaska in silty muds at depths greater than 100 m.

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### LITERATURE CITED

- BUCKLAND-NICKS, J. & F.-S. CHIA. 1989. Spermiogenesis in *Chaetoderma* sp. (Aplacophora). *Journal of Experimental Zoology* 252:308-317.
- HEATH, H. 1911. The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific ... by the "Albatross. ..." *Memoirs of the Museum of Comparative Zoology* (Harvard University) 45(1):1-179 + 40 pls.
- IVANOV, D. I. 1981. [*Caudofoveatus tetradens* gen. et. sp. n. and diagnosis of taxa in the subclass Caudofoveata (Mollusca, Aplacophora)]. *Zoologicheskii Zhurnal* (Akad. Nauk SSSR) 60:18-28 [in Russian].
- IVANOV, D. I. 1984. [Caudofoveats (Mollusca, Caudofoveata) in Peter the Great Bay]. Pp. 28-41. In: A. I. Kafanov (ed.), [*Hydrobiological research of bays and inlets of Primorye*]. Far East Science Center, USSR Acad. Sci., Vladivostok [in Russian].
- KATHMAN, R. D., R. O. BRINKHURST, R. E. WOODS & S. F. CROSS. 1984. Benthic studies in Alice Arm, B.C., following cessation of mine tailings disposal. *Canadian Technical Report of Hydrography and Ocean Sciences* No. 37, 57 pp.



- KATHMAN, R. D., R. O. BRINKHURST, R. E. WOODS & D. C. JEFFRIES. 1983. Benthic studies in Alice Arm and Hastings Arm, B.C. in relation to mine tailings dispersal. Canadian Technical Report of Hydrography and Ocean Sciences No. 22, 30 pp. + appendices.
- SALVINI-PLAWEN, L. V. 1978. The species-problem in Caudofoveata (Mollusca). *Zoologischer Anzeiger* 200:18-26, figs. 1-10.
- SALVINI-PLAWEN, L. V. 1984. [Comments on *Chaetoderma* and *Crystallophrisson* (Mollusca, Caudofoveata)]. *Zoologicheskii Zhurnal* 63:171-175 [in Russian].
- SCHELTEMA, A. H. 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere* 72:361-370.
- SCHELTEMA, A. H. 1973. Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere* 76:97-107.
- SCHELTEMA, A. H. 1976. Two new species of *Chaetoderma* from off west Africa (Aplacophora, Chaetodermatidae). *Journal of Molluscan Studies* 42:223-234.
- SCHELTMA, A. H. 1989. Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off southeastern Australia. *Records of the Australian Museum* 41:43-62.
- SCHWABL, M. 1963. Solenogaster mollusks from southern California. *Pacific Science* 17:261-281.
- STORK, H. A. 1941. Solenogastren der Siboga-Expedition. *Siboga Expeditie* 47b:45-70.
- [U.S.] BUREAU OF FISHERIES. 1906. Dredging and hydrographic records of the U.S. Fisheries Steamer Albatross for 1904 and 1905. Report of the Commissioner of Fisheries for the Fiscal Year 1905 and Special Papers, Bureau of Fisheries Document No. 604, 80 pp.
- U.S. COMMISSION OF FISH AND FISHERIES. 1905. Records of dredging and other collecting and hydrographic stations of the Fisheries Steamer Albatross in 1903. Report of the Commissioner of Fisheries for the year ending June 30, 1903, 29:123-138.



## APLACOPHORA AS A TETHYAN SLOPE TAXON: EVIDENCE FROM THE PACIFIC

*Amélie H. Scheltema*

### ABSTRACT

Recent aplacophoran collections from the Pacific yield information on global distributions of this class of Mollusca. A former Tethyan or pre-Tethyan distribution is suggested by the disjunct occurrence of five species which form a subgroup within the genus *Falcidens*, two from the western Atlantic and three from the western Pacific; by three species of the genus *Prochaetoderma* with a similar disjunct distribution; and by the broadly distributed family Pararrhopalidae. High diversity of species and less than 40% numerical dominance by any one species typify samples from slope stations off southeast Australia, whereas low diversity and dominance greater than 60% typify the shelf in Bass Strait; the latter may reflect the disruptive effects of Pleistocene regression of sea level. Three species pairs with one of each pair occurring on the slope and the other on the shelf may indicate that shelf species evolved from slope species. A new genus with eight species, seven from slope and abyssal hydrothermal vents, is comprised of six species from slope depth and two from abyssal depths; the abyssal species have character states derived from the shallower species. The evidence from present-day distributions of species, genera, and families indicates that the Aplacophora were already widespread on continental slopes by Tethyan times.

Aplacophoran mollusks are primarily deep-water forms and only with the advent of precision depth finders and adequate collecting gear—box cores, grabs, and epibenthic sleds used in conjunction with small-meshed screens—have they been collected in numbers that represent their actual occurrence. The numbers of specimens and species in samples taken at the turn of the century mostly with coarse-meshed trawls can be contrasted with those now being taken (Table 1). For instance, the SIBOGA Expedition to the East Indies in 1899–1900 collected 66 aplacophoran specimens and about 13 species from 28 dredgings between 22 m and over 3,000 m (Nierstrasz, 1902; Stork, 1941), whereas a single epibenthic sled sample taken in 1986 from the continental slope at 400 m off southeast Australia yielded 536 specimens and 22 species. In 1906, the ALBATROSS dredged 11 specimens of a single species from slope depths at 868 m in the Aleutians (Heath, 1911), but in 1970, 31 specimens of another species were taken in a  $\frac{1}{4}$ -m<sup>2</sup> spade box core from hadal depths at 7,298 m in the Aleutian Trench, an astounding density of 124·m<sup>-2</sup> (Scheltema, 1985).

Notwithstanding the inadequacies of sampling by earlier dredging efforts, the data that have accumulated since the CHALLENGER took a single specimen off the Philippines in 1875 (Selenka, 1885) indicate a rich and diverse aplacophoran fauna in the Pacific from depths of 10 m to over 7,000 m, even though fewer than 3,600 specimens exist in collections or have been described from the entire Pacific. More than one-third of these have come from recent surveys off southeast Australia, and more than 700 were taken from areas of hydrothermal vents. Aplacophora have been collected from a wide variety of habitats: from the shelf beneath the cold waters of the north Pacific and from the tropical Great Barrier Reef and New Caledonia; from vent regions; from sea mounts; from the vast abyssal, oligotrophic regions of the central north Pacific; interstitially from sand; from shallow areas with cyclic physical disturbance and from slope, abyssal and

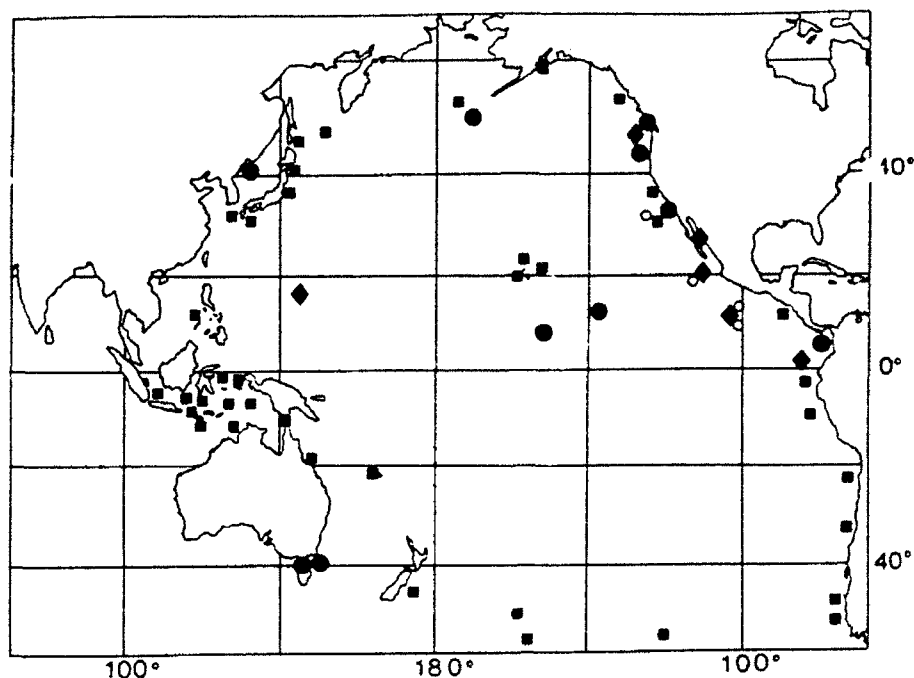


Figure 1. Pacific Ocean locations from which aplacophorans have been collected. Large solid circles: areas recently surveyed using epibenthic sleds and quantitative gear or, in the case of hadal depths greater than 5,000 m, by a single box-core collection; all samples sieved through fine-mesh screens; squares: localities represented by a single or a few non-quantitative samples; diamonds: hydrothermal vent locations sampled from a submarine; small open circles: sea mounts (guyots) sampled from a submarine (cf. Tables 1, 3).

hadal regions of great stability (Fig. 1; Table 1; and unpublished data). Species vary in size from the large, stout *Neomenia yamamotoi* (100 mm by 35 mm; Baba, 1975) and the long, cylindrical *Epimenia verrucosa* (300 mm by 10 mm; Baba, 1939) to numerous species less than 5 mm in length.

Patterns of distribution are discernible within this great diversity of morphology and habitat. This paper suggests what some of these patterns are and the evidence for them: (1) many Aplacophora at slope depths (between 200 and 3,000 m) have distributions that are at least as old as Tethys; (2) new species have evolved on the continental shelf (subtidal to 200 m) and in the abyss (3,000 to 5,000 m) from colonization upward and downward from the slope respectively; (3) the high diversities on the slope and low diversities on the continental shelf reflect disturbance of the shelf fauna by Pleistocene regression of sea level.

#### MATERIALS

Specimens examined were from the Pacific surveys and expeditions marked by section marks in Table 1. Several samples from the western Atlantic taken by Woods Hole Oceanographic Institution ships also provided information: R.V. CHAIN Cruise 58 Sins 96 (136+ specimens) and 105 (105 specimens), and R.V. KNORR Cruises 25 Sins 295, 297 (66 specimens) and 35 Sin 346 (190+ specimens). Other western Atlantic samples used were from Duke University (1965) Sins 351, 2361, 2732, and 3417 (14 specimens); and from the Instituto de Biologia, Universidade Federal do Rio de Janeiro (9 specimens).

Table 1. Major expeditions and surveys which have collected Aplacophora in the Pacific (cf. Fig. 1)\*

Survey/expedition†	Date	Location/depth m	Specimens (No.)	Species‡ (No.)	Authors, if published
SIBOGA Exp.	1899-1900	East Indies 18-3,088	66	~13	Nierstrasz, 1902; Stork, 1941
ALBATROSS Exp.	1891, 1902	off Hawaii 9-275	18	7	Heath, 1911
ALBATROSS Exp.	1892, 1906	No. Pacific, Kuriles, Alaska 122-868	17	3	Heath, 1911
ALBATROSS Exp.	1897, 1904	off so. California 38-3,953	199	10	Heath, 1911
ALBATROSS Exp.	1903	So. Alaska (panhandle) 90-527	22 + "several"	3	Heath, 1911
ALBATROSS Exp.	1906	off Japan 185-413	18	7	Heath, 1911
Allan Hancock Pacific Exp.	1952-1957	off so. California 33-1,102	283	14	Schwabl, 1963
VEMA Exp., U.S. Antarctic Res. Pgm	1958-1961, 1964	off Central, So. America 626-5,834	11	3	Salvini-Plawen, 1972, 1978
U.S. Antarctic Res. Pgm	1964-1966	So. Pacific 146-3,694	39	9	Salvini-Plawen, 1978
Univ. Oregon§	1962-1967	off Oregon 100-2,900	276	~12	unpubl.
SSR Academy Nauk	1970	Peter the Great Bay 120	42	4	Ivanov, 1984
SEVENTOW	1970	Aleutian Trench 7,298	31	1	Scheltzema, 1985
DOMES Project	1975-1976	mid-Pacific 4,985-5,117	3	1	Scheltzema, 1985
So. California§ Bight Pgm	1976	off Los Angeles, California	143+	10+	unpubl.
SEATECH§	1981	off British Columbia 107-175	205	3	unpubl.
DSRV ALVIN	1981-1982	Panama Basin 4,000	59	~5	Scheltzema, 1985 (part)
Bass Str. Sur- vey,§ Mus. Victoria	1980-1983	Bass Strait <200	382	~25	Scheltzema, 1989 (part)
CSIRO-FRS- 86§	1986	Slope off SE Australia 363-1,850	937	>40	Scheltzema, 1989 (part)

\* Single species or specimens not included in the table but indicated on Figure 1 are described in Selenka (1985). Phylloporina: Thayer (1897, 1902, Torres Strait, n.w. Australia; East Indies); Ponder (1970, off New Zealand); Baba (1940, 1971, Japan); Ogasawara (1941, Japan); Ogasawara and Taniguchi (1976, Chile); Morse (1979, Puger Sound, intermittent). Species to be described have been taken from sea mounts in the eastern Pacific (13 specimens, 7 spp.), from Panama Bay (25 specimens, 1 spp.), from New Caledonia (4 specimens, 2 spp.), and from the Great Barrier Reef (11 specimens, 2 spp.). Most of the more than 700 specimens and 14 species from hydrothermal vents are listed in Table 3.

† CSIRO = Australian Commonwealth Scientific and Industrial Research Organization; SEVENTOW = R/V *Melville Cruise 70*, Scripps Institution of Oceanography; DOMES was a project under the National Oceanographic and Atmospheric Administration, U.S. Department of Commerce; SEATECH was a project under the Canadian Department of Fisheries and Oceans; So. California Bight Pgm was under Minerals Management Service, U.S. Department of Interior.

‡ Species known or suspected to be synonyms in *Siboga*, *Albatross*, and Allan Hancock samples are not included. The same species may occur in more than one collection.

§ Collections with unpublished species examined for the present paper.

## TAXONOMIC CHARACTERS

The main characters used to discriminate species and higher taxa in both aplacophoran subclasses Chaetodermomorpha and Neomeniomorpha are body shape and proportions, position of spicules in the integumental cuticle, and spicule and radula morphology; in addition, the anatomy of the reproductive system, including the morphology of copulatory spicules, and type of salivary glands are taxonomic characters used in differentiating the hermaphroditic Neomeniomorpha.

## APLACOPHORA AS A TETHYAN FAUNA OF THE SLOPE

The present-day distribution of aplacophorans has existed at least since Tethys, before the Atlantic and Pacific were isolated from each other. The evidence comes both from families with widespread slope distributions and from genera with disjunct Atlantic and Pacific distributions on slopes at mid-latitudes. The evidence that this ancient aplacophoran fauna existed primarily at slope depths, just as it does today, is the greater diversity of slope over continental shelf species, probably reflecting the stable environment of the former. Speciation appears to have occurred vertically in both upward and downward directions from the slope.

*Evidence for Tethyan distribution.*—Two genera in the subclass Chaetodermomorpha, the burrowing aplacophorans (Fig. 2A), and one family in the Neomeniomorpha, the creeping, cnidarian-eating aplacophorans (Fig. 5A, B), are presented here as examples of Tethyan groups.

The chaetoderm genus *Falcidens* contains a subgroup of five species that are closely related in body shape and in unique spicule ornamentation of crossed diagonal ridges (Fig. 2). Two of these species, still unnamed, are from the western Atlantic (Fig. 2C), one from the slope, one from the shelf; and three are from the western Pacific: the slope form *Falcidens loveni* (Nierstrasz) from Indonesia, the shelf species *F. chistos* Scheltema off southeast Australia (1989), and a third unnamed slope species also off southeast Australia (Fig. 2B). No member of this subgroup has so far been found in the east Pacific, where a number of other *Falcidens* species are known to occur (Schwabl, 1963; Scheltema, unpubl.). Such a unique spicule morphology is interpreted as an autapomorphy, that is, a derived character for this subgroup, and their present disjunct distribution must have resulted from a time when there was free access between the Atlantic and Pacific Oceans.

Another genus of Chaetodermomorpha with a disjunct distribution is *Prochaetoderma*, distinguished from other Prochaetodermatidae by the spicules which are flat with a base shorter than a broad, triangular blade bearing a median keel and sharp distal point (Fig. 3A, B). There are two published species: *P. raduliferum* from the shelf and slope of the Mediterranean (Kowalevsky, 1901; Salvini-Plawen, 1977), and *P. yongei*, an upper slope species widely distributed along the continental margins of the northwest, northeast and southeast Atlantic, but missing in the western Atlantic south of 34°N (Scheltema, 1985). A third species still to be named has recently been dredged from the slope off southeast Australia (Scheltema, 1989). The family Prochaetodermatidae is known from the east Pacific, but not the genus *Prochaetoderma* (Scheltema, unpublished data; Schwabl, 1963, published a species of *Spathoderma* as *Prochaetoderma californicum*).

Among the Neomeniomorpha the family Pararthopalidae has a widespread distribution on continental slopes of the Atlantic, Pacific, and Antarctic Oceans; the family is characterized here by the presence of fishhook-like spicules (Fig. 3C). The first three species described in this family—*Pruvotina impexa* (Pruvot,

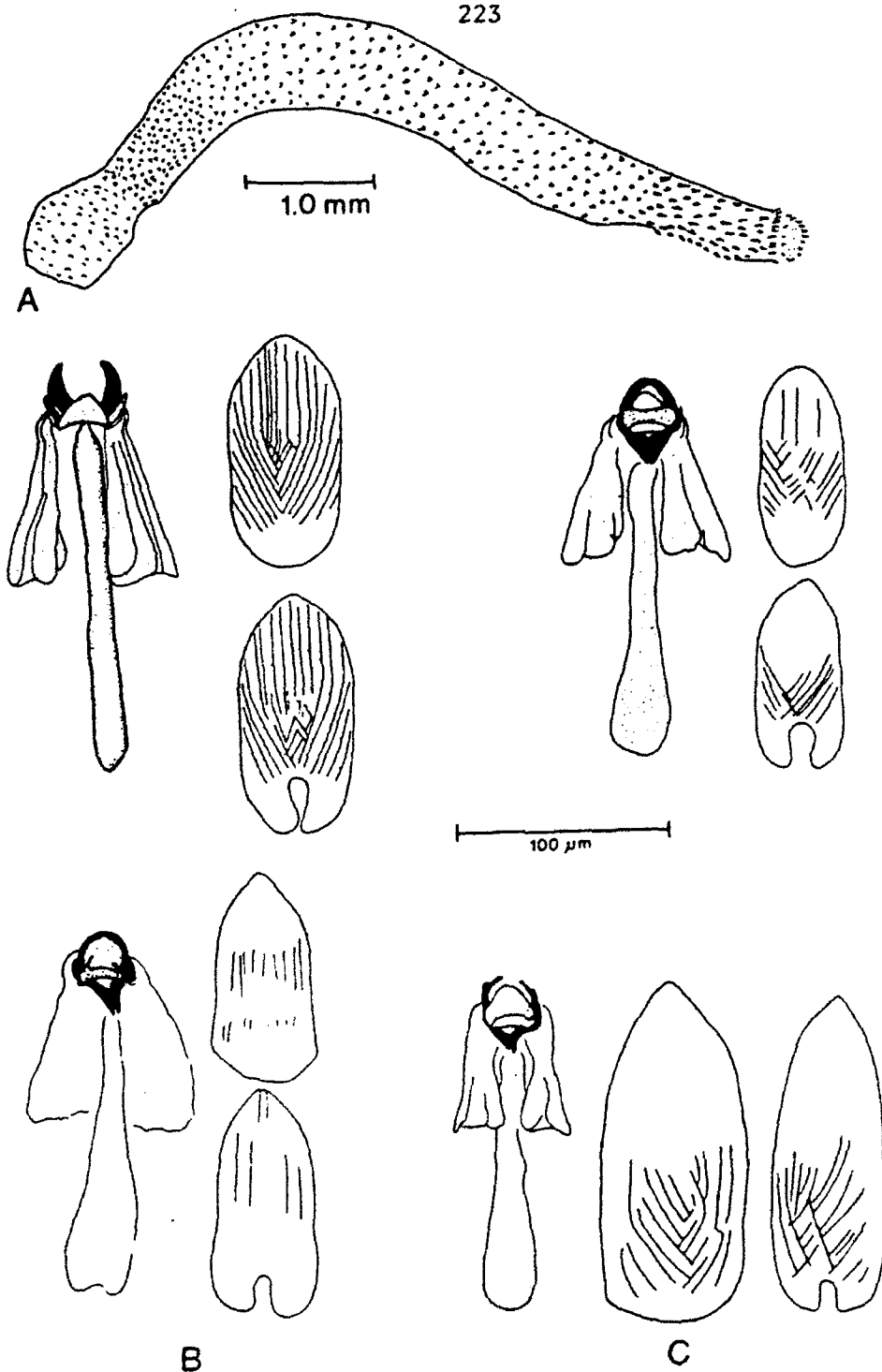


Figure 2. Tethyan *Falcidens* group with spicules bearing crossed diagonal ridges. A: Entire specimen of *F. chiasos* showing body shape. B: Radula and spicules from two west Pacific species off southeast Australia, *F. chiasos* above, new species below. C: two new species from the west Atlantic. The two upper species are from the continental shelf at depths less than 200 m; the two lower species are from the slope between 400 and 1,000 m. (A and B, left, from Scheltema, 1989.)

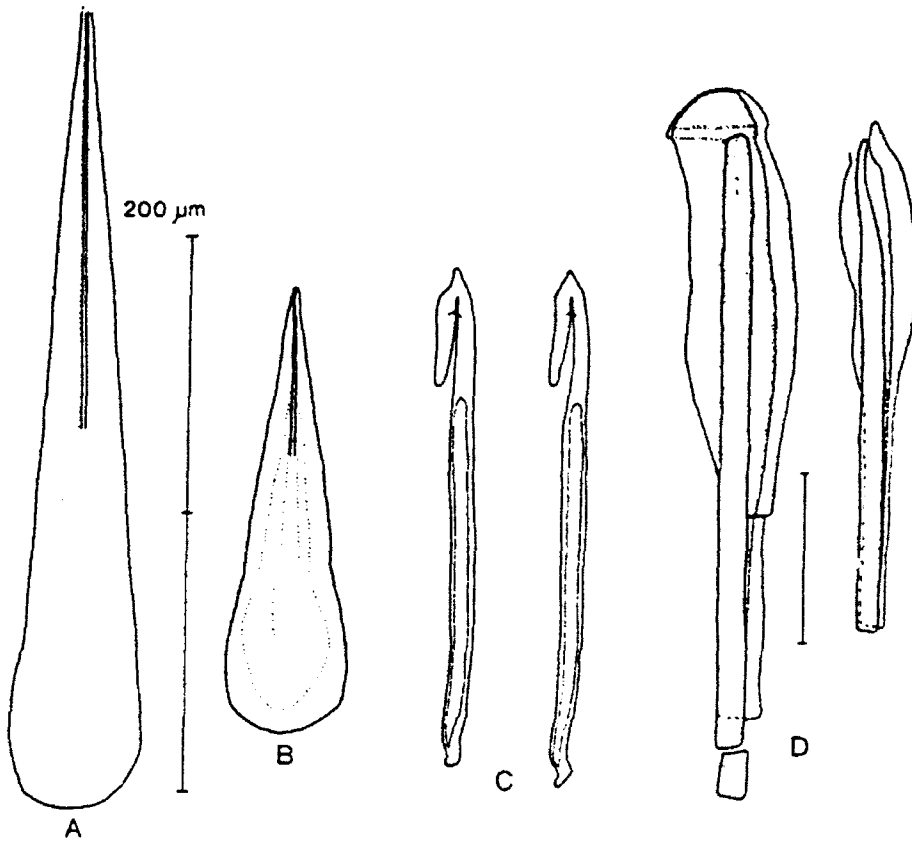


Figure 3. Spicules of A: *Prochaetoderma* sp. from the slope off southeast Australia; B: *Prochaetoderma yongei* Scheltema of the east and west Atlantic slopes; and C: an unnamed species in the family Pararrhopalidae. D: copulatory spicules which differentiate two unnamed species of *Eleutheromenia* (Pararrhopalidae) from off southeast Australia, shelf species on the left, slope species on the right; scale line = 200  $\mu$ m.

*Eleutheromenia sierra* (Pruvot), and *Pararrhopalia pruvoti* Simroth (as "*Proneomenia vagans*")—were from shelf depths in the Mediterranean (Pruvot, 1891). All other published species in this family are from the Antarctic or Subantarctic (Thiele, 1913; Salvini-Plawen, 1978), although many new species from the eastern and western Atlantic await description.

The family Pararrhopalidae forms a particularly numerous and diverse group off southeast Australia, often comprising more than one-half the total number of Neomeniomorpha at any one slope location (Table 2). It is also a dominant but much less diverse group in the Antarctic. The slope fauna of the northeast United States contrasts sharply with that of southeast Australia with only one or two species belonging to the Pararrhopalidae in each of three selected large samples. (Methods of sampling used in the Antarctic were not the same as those off southeast Australia and northwest United States and thus may not be comparable.)

The genus *Eleutheromenia* is probably represented off southeast Australia by two new species (Fig. 3D), but as the Mediterranean type species of this genus is not known from recent collections and was originally inadequately described (Pruvot, 1891), the affinity is not certain. Even though a disjunct distribution is



Table 2. Numbers of Neomeniomorpha, Pararrhopalidae,\* and species of Pararrhopalidae from the slope off southeast Australia, in the Antarctic and sub-Antarctic, and from off northeast United States

Depth† m	Neomeniomorpha† (No.)	Pararrhopalidae (No.)	Species of Pararrhopalidae (No.)
Off southeast Australia			
363	12	1	1
400	513	398	9
400	13	1	1
720	27	15	3
770	16	4	3
800	28	20	5
800	56	33	6
951	34	15	6
1,000	64	26	6
1,500	18	5	3
Antarctic and Sub-Antarctic			
148-201	66	26	2
210-220	24	16	5
311-426	18	4	2
342-360	12	7	2
344-351	58	13	2
Off northeast United States			
457	190+	35	1
498	136+	88	2
530	105	12	1

\* Family here defined as Pararrhopalidae with hooked spicules, whether solid or hollow, and includes the genera *Pararrhopalia* Simroth, *Pruvotina* Cockerell, *Lituiherpia* Salv.-Pl., *Ocheyoherpia* Salv.-Pl., *Gephyroherpia* Salv.-Pl., *Labidoherpia* Salv.-Pl., and *Eleutheromenia* Salv.-Pl.

† Only stations at depths greater than 200 m included. Australian samples are from National Museum of Victoria slope stations. Antarctic samples are from U.S. Antarctic Research Program (USARP) stations (data from Salvini-Plawen, 1978); stations off United States are from Woods Hole Oceanographic Institution cruises *Chain 58* and *Knorr 35*. Australian and United States samples were taken with epibenthic sled; USARP collecting gear unknown.

‡ Only stations with 12 or more Neomeniomorpha included.

not yet certain for this genus of Pararrhopalidae, the wide geographic range of the family on continental slopes of the Pacific, Atlantic, and Antarctic Oceans suggests a previous Tethyan distribution.<sup>1</sup>

**High Diversity of Slope Fauna.**—Few surveys offer the opportunity to compare continental shelf and slope faunas as well as the recent surveys in Bass Strait and the slope off southeast Australia under the direction of the Museum of Victoria, Victoria Institute of Marine Science, and the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO). These surveys afford the opportunity to compare (1) faunal diversities on each side of the break between the shelf and slope and (2) slight differences in morphology of particular species over short horizontal and vertical distances.

A comparison of faunal diversities shows that the Aplacophora have undergone their greatest evolutionary radiation on the slope. Analyses of three epibenthic sled samples taken at depths of 70, 140, and 400 m are shown in Figure 4. Each represents the largest sample of aplacophorans collected by epibenthic sled from shelf depths at less than 100 m and between 100 and 200 m, and from the upper

<sup>1</sup> A further example of a Tethyan distribution has come to light since the preparation of this manuscript. The genus *Tegulioherpia* is represented by two described species from the Mediterranean (*T. myodoryza*, *T. stimulosa*) and by one described species in Bass Strait off southeast Australia (*T. tasmanica*) (Salvini-Plawen, 1988). Four additional species from Bass Strait remain to be described (Scheltema, in press).

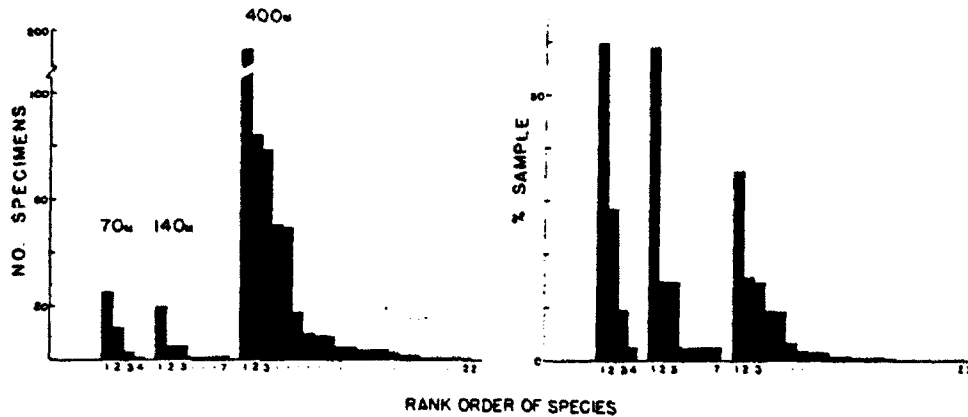


Figure 4. Faunal diversity and species dominance in the aplacophoran fauna on the continental shelf and slope off southeastern Australia. Each species in a sample is ranked along the abscissa from most to least numerous by number of specimens (left graph) and by percent of sample (right graph). The graph of each depth represents the largest sample of aplacophorans taken by epibenthic sled in the depth ranges of (1) less than 100 m, (2) 100–200 m, and (3) greater than 200 m; the samples are not quantitative and cannot be compared directly. Samples from Museum of Victoria: 40 m, Stn 155 Bass Strait; 140 m, Stn 170 Bass Strait; 400 m, Slope Stn. 40.

slope at depths greater than 200 m. In the upper graph, the number of specimens (ordinate) of each species ranked from the most to least numerous (abscissa) is shown; the right graph translates the actual numbers of ranked species into percent of the total sample. At 70 and 140 m on the shelf, species were few, 4 and 7, respectively, but dominance was high, the first-ranked species in each case accounting for nearly 60 percent of the sample. At 400 m on the slope, the number of species is 22, 3 to 5 times greater than on the shelf, and dominance is much lower, the first-ranked species accounting for less than 40 percent of the total sample.

High dominance and low diversity of species on the shelf is inferred to be the result of Pleistocene regression of sea level when much of the shelf became terrestrial and of subsequent recolonization after the sea was restored to its present level. The total number of specimens at the three stations cannot be compared quantitatively because epibenthic sleds do not yield quantitative samples.

*Colonization and Evolution of Species Upslope.*—Three pairs of closely related aplacophoran species suggest a post-Pleistocene recolonization of the shelf from the slope and subsequent speciation. The examples come from two of the Tethyan groups described above.

The *Falcidens* group with cross-ridged spicules is represented in the western Atlantic by an undescribed slope species at depths of 445 to 1,000 m from off Pt. Lookout, North Carolina, to the Guiana Basin off northeast South America (Fig. 2C, lower). A second undescribed species occurs at less than 200 m off Rio de Janeiro, Brazil (Fig. 2C, upper). This pair of Atlantic species is paralleled by another such pair half way around the world off southeast Australia (Fig. 2B), an undescribed slope species and its shelf counterpart, *F. chistos* (Scheltema, 1989).

Two still undescribed species of *Eleutheromenia*, one from the shelf, the other from the slope off southeast Australia, are so similar that only distinct, nonoverlapping differences in the morphology of the copulatory spicules can positively distinguish them (Fig. 3D). Their distributions overlap between 120 and 130 m.

Table 3. Eight species of a new genus of Neomeniomorpha from eastern and western Pacific vent regions and the abyss off western South America

Location	Depth m	Species	Specimens (No.)
<b>Slope</b>			
Galapagos (vents) 0°35'–48°N, 86°05'–14°W	2,450	<i>New genus</i> sp. <i>a</i> <i>New genus</i> sp. <i>r</i>	40 23
East Pacific Rise (vents) 12°48'N, 103°56'W 20°50'N, 109°06'W	2,620 2,620	<i>New genus</i> sp. <i>g</i> <i>New genus</i> sp. <i>a</i> <i>New genus</i> sp. <i>b</i> <i>New genus</i> sp. <i>s</i>	6 50 8 24
Juan de Fuca Ridge (vents) 47°57.1'N, 129°06.0'W	2,250	<i>New genus</i> sp. <i>j</i>	447
Explorer Ridge (vents) 49°45.8'N, 130°15.8'W	1,800	<i>New genus</i> sp. <i>j</i>	107
<b>Abyss</b>			
Mariana Back-Arc Basin (vents) 18°12.6'N, 144°42.4'E	3,640	<i>New genus</i> sp. <i>i</i>	5
Peru-Chile Trench 7°35'S, 81°24'W	5,820	" <i>Simrothiella</i> " <i>schizoradulata</i> (Salvini-Plawen) [= <i>New genus</i> ]	1*

\* Seven additional specimens were taken in the Antarctic from the abyss off the south Shetland Islands (Salvini-Plawen, 1978).

the lower depth limit for the shelf species; the slope species extends from 120 to 400 m.

Although there is no morphological evidence to indicate which species gave rise to the other in these three morphologically similar pairs, it is hypothesized that the species from the stable slope are the older. The hypothesis rests on three considerations: (1) slope species are of Tethyan or pre-Tethyan age and more diverse than shelf species and thus could act as a source over time; (2) the species pairs are so similar that recent, i.e., post-Pleistocene, splitting of the shelf from the slope species seems probable; and (3) the close parallel in evolution between the disjunct western Atlantic and western Pacific *Falcidens* species pairs appears to be based on the same global event and reflect the same evolutionary process. The hypothesis can be tested by further systematic work to discover primitive and derived character states in other species pairs.

*Evidence for Colonization and Evolution of Species Downslope.*—A new genus of Pacific aplacophorans (cited as *Simrothiella* in Turner, 1985) with a helically turned radula contains eight species. Seven species are unnamed; they occur in hydrothermal vent regions, six of them at slope depths and one at depths greater than 3,000 m (Table 3). The eighth species, placed originally in the genus *Simrothiella* as *S. schizoradulata* (Salvini-Plawen, 1978), is also abyssal.

Four characters show derived states in one or the other of the two abyssal species: body form, spicules, spicule position, and radula. The polarity of these character states is judged either by considering the most usual state among Neomeniomorpha as primitive, with more than one taxon containing members with the same derived state as a result of parallel evolution, or by considering the less complex, regular structure as primitive to the more complex and irregular. Ontogenetic and fossil evidence is lacking.

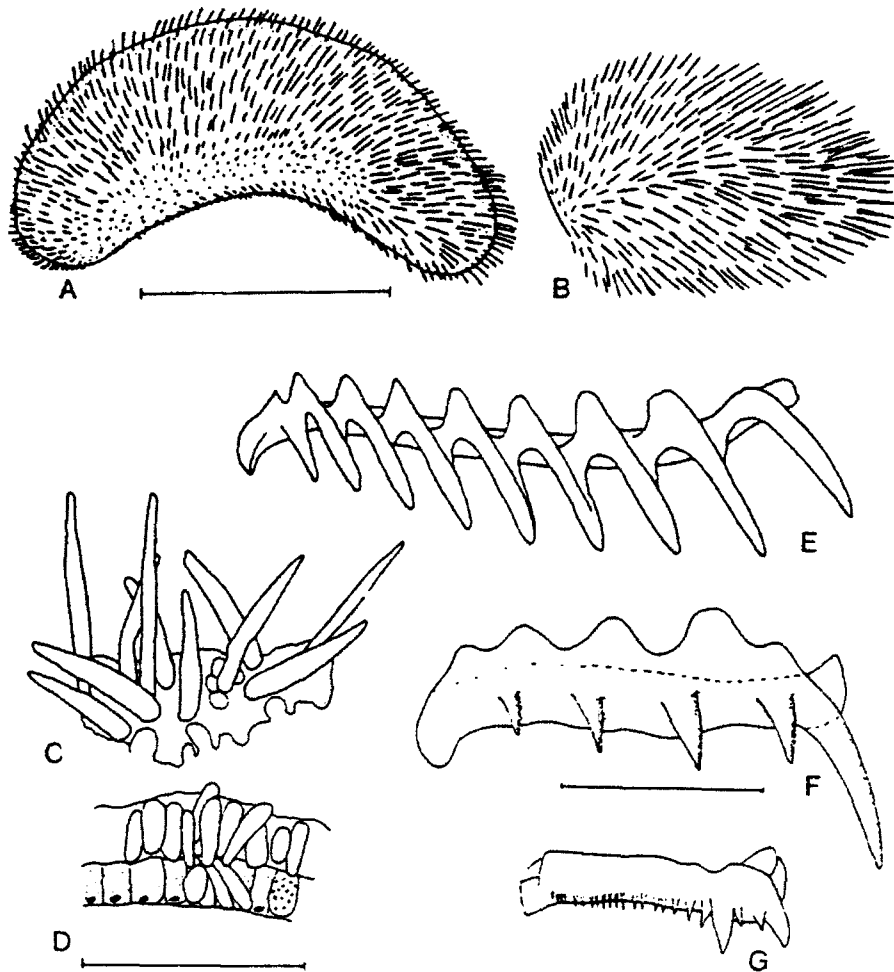


Figure 5. Primitive and derived states in a new genus in the subclass Neomeniomorpha (cf. Table 3). A: Slope species *a*, primitive elongate oval shape; B: abyssal "*Simrothiella*" [=New genus] *schizoradulata* (Salvini-Plawen), derived ball-shaped body; C: slope species *a*, primitive spicule position with spicules erupted through the cuticle; D: abyssal species *i*, derived spicule position with spicules retained within the cuticle; E: slope species *b*, primitive radula tooth with denticles of even length; F: slope species *a*, derived radula tooth with a single, long lateral denticle; G: abyssal species "*S.*" *schizoradulata*, derived tooth with complex lateral denticular process. (E from Scheltema, 1988.) Scales: A = 1.0 mm (A, B); D = 0.1 mm (C, D); F = 0.4 mm (E-G).

The body shape is primitively an elongate oval, that is, worm-shaped: the derived shape is ball-like (Fig. 5A, B). Primitively the spicules are solid; hollow spicules are derived. Spicules extend beyond the surface of the cuticle primitively; in the derived state they remain mostly unerupted within the cuticle (Fig. 5C, D). The radula tooth changes from having nearly even-sized denticles to having a single, longer lateral denticle, and from a simple lateral to a more complex, reinforced lateral with several denticles (Fig. 5E, F, G). The abyssal vent species *i* in the Mariana Back-Arc Basin maintains primitive states in all characters except the derived position of spicules unerupted within the cuticle. In the abyssal "*S.*" *schizoradulata* (Fig. 5B), all character states except spicule position are derived.

The existence of derived character states in the two abyssal species is understood here to show evolutionary change from downslope colonization into the abyss.<sup>2</sup>

### DISCUSSION

Collections of Aplacophora have been made for the last one hundred years; they have shown that these animals live primarily at slope depths. For instance, among Pacific Chaetodermomorpha, 8 species are restricted to the continental shelf and 43 species are slope or abyssal species (Scheltema, 1989, Table 2). Differences in number and diversity between adjacent shelf and slope regions can be shown wherever collections have been made using comparable gear and sieving processes (Fig. 4).

Evolution of species downwards from slope depths seems to have occurred in some groups as described above, if the criteria for determining primitive and derived character states are accepted. In other groups the evidence is not so clear. For instance, in the Prochaetodermatidae four species comprise the genus *Chev- roderma* (Scheltema, 1935). Two are widespread abyssal species, *C. whitlatchi* in the Pacific and *C. turnerae* in the Atlantic. The third, *C. gausson*, is an abyssal species restricted to the West European Basin, and the fourth, *C. scalpellum*, is a slope species of limited geographic range in the eastern Atlantic. Primitive and derived character states are not obvious among these four species, nor among the four named genera of the family (Scheltema, 1985; 1989).

It seems plausible that slope species have given rise to shelf species for the reasons stated above, but polarity of character states in morphologically similar species from the two depth zones remains to be discovered.

The Aplacophora are a small taxon, widespread both geographically in all the world oceans and vertically from shallow to hadal depths. Few species and small genera combined with enormous ranges on the one hand and the presence of geographically close sister species on the other provide an unusual opportunity to gain insights from relatively few species. The effort to collect and carefully sort deep-sea animals, however, remains large, time-consuming, and expensive, and thus very little is yet known of the Pacific deep-sea aplacophoran fauna.

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I thank C. C. Lu of the Museum of Victoria and Winston Ponder of the Australian Museum, Sydney, for sending me the aplacophoran collections in their museums. Thanks are also extended to R. Silva Absalao, Universidade Federal do Rio de Janeiro, for providing the sample of *Falcidens* off Rio de Janeiro. Samples from RV KNORR Cruise 35 and RV CHAIN 58 were collected under National Science Foundation grant GA31105 and provided to me through the kindness of H. L. Sanders. Specimens from the hydrothermal vents were provided by the following persons to whom my thanks are extended: Robert R. Hessler, Scripps Institution of Oceanography; Verena Tunnicliffe, University of Victoria; the late Joseph Rosewater, Smithsonian Institution; M. Segonzac, Centre National de Tri d'Océanographie Biologique (CENTOB, Brest); H. L. Sanders and J. Frederick Grassle, Woods Hole Oceanographic Institution. Without the effort of these individuals and of the many more not named here who have organized expeditions, collected, sieved and sorted, and without the support of their institutions, synoptic accounts of deep-sea taxa by the systematist would be impossible.

<sup>2</sup> Since preparing this paper, the author has recognized specimens from 2,091 m in the northeast Atlantic which are nearly indistinguishable from "*S. schizoradulata*" Salvini-Plawen. It has not yet been determined whether these specimens belong to the same or to a new species or whether similar specimens occur in other Atlantic collections. "*S. schizoradulata*" also occurs abyssally at 4,700 m at 61°S, 61°W off the South Shetland Islands just between the Atlantic and Pacific Oceans (Salvini-Plawen, 1978). The existence of a similar or the same species on the northeast Atlantic slope complicates the hypothesis for derivation of "*S. schizoradulata*" by downslope colonization from a Pacific slope taxon.

Finally, thanks are extended to A. J. Kohn, University of Washington, for inviting me to participate in the recent symposium on Indo-Pacific Molluscan Biogeography and Evolution; and to R. S. Scheltema for reading the manuscript.

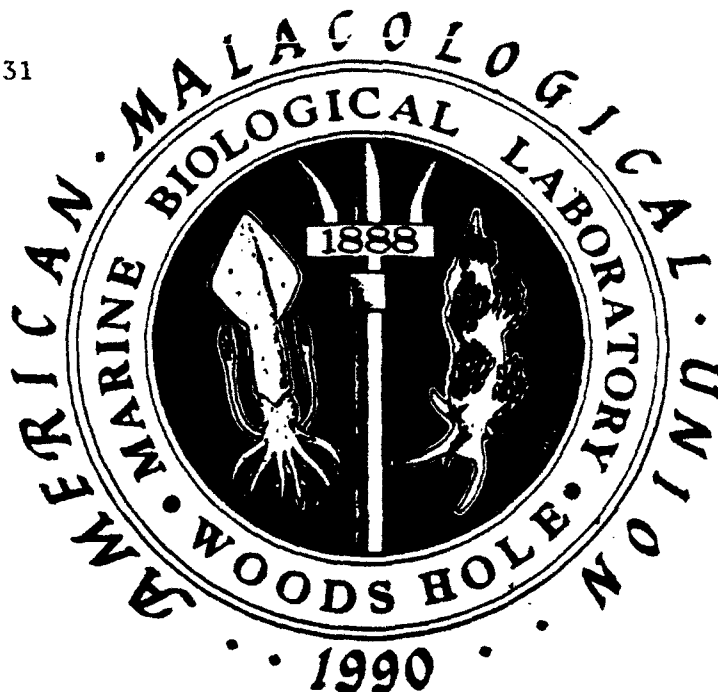
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### LITERATURE CITED

- Baba, K. 1939. Preliminary note on *Epimenia verrucosa* (Nierstrasz), a solenogastre species from Amakusa, Japan. *Venus (Tokyo)* 9: 35-42.
- . 1940. *Epimenia ohshimai* a new solenogastre species from Amakusa, Japan. *Venus (Tokyo)* 10: 91-96.
- . 1975. *Neomenia yamamotoi* spec. nov., a gigantic solenogaster (Mollusca: Class Solenogastres, Family Neomeniidae), occurring in the northeastern part of Japan. *Publ. Seto Mar. Biol. Lab.* 22(5): 277-284.
- Heath, H. 1911. The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific . . . by the "Albatross". . . . *Mem. Mus. Comp. Zool.* 45(1): 17-179.
- Ivanov, D. I. 1984. Caudofoveats (Mollusca, Caudofoveata) in Peter the Great Bay. Pages 28-41 in A. I. Kafanov, ed. *Hydrobiological research of bays and inlets of Primorye*. Far East Science Center, USSR Acad. Sci., Vladivostok. (In Russian)
- Kowalevsky, A. 1901. Sur le genre *Chaetoderma*. *Arch. Zool. Exp.* (3)9: 261-284.
- Morse, M. P. 1979. *Meiomenia swedmarki* gen. et sp. n., a new interstitial solenogaster from Washington, USA. *Zool. Scripta* 8: 249-253.
- Nierstrasz, H. F. 1902. The solenogastres of the Siboga-Expedition. *Siboga-Exped.* 47. E. J. Brill, Leyden. 46 pp.
- Okuda, S. 1943. The fauna of Akkeshi Bay. XIV. Solenogastre. *Annot. Zool. Jap.* 22: 11-14.
- Osorio R., C. and E. Tarifeño. 1976. A new species of aplacophorous mollusk from the southeastern Pacific Ocean: *Chaetoderma araucanae* spec. nov. (Mollusca: Caudofoveate: Chaetodermatidae). *Veliger* 19: 84-89.
- Ponder, W. F. 1970. A new Aplacophoran from New Zealand. *J. Malac. Soc. Australia* 2(1): 47-54.
- Pruvot, G. 1891. Sur l'organisation de quelque néoménies des côtes de France. *Arch. Zool. Exp.* (2)9: 699-806.
- Salvini-Plawen, L. v. 1972. Die Caudofoveata des Mittelmeeres und das Genus *Scutopus* (Mollusca, Aculifera). Pages 27-51 in B. Battaglia, ed. *Fifth European Marine Biology Symposium* Piccin Editore, Padua.
- . 1977. Caudofoveata (Mollusca). Priapulida und apode Holothurien (*Labidoplax*, *Myriotrochus*) bei Banyuls und im Mittelmeer allgeheim. *Vie-Mil* 27A: 55-81.
- . 1978. Antarktische und subantarktische Solenogastres (eine Monographie: 1896-1974). *Zoologica (Stuttgart)* 44: 1-315.
- . 1988. Einige Solenogastres (Mollusca) der Europäischen Meiofauna. *Ann. Naturhist. Mus. Wien* 90(B): 373-385.
- Scheltema, A. H. 1985. The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca: Chaetodermomorpha). *Biol. Bull. (Woods Hole)* 169: 484-529.
- . 1988. Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. *Amer. Mole. Bull.* 61: 57-68.
- . 1989. Australian aplacophoran molluscs: I. Chaetodermomorpha from Bass Strait and the continental slope off southeastern Australia. *Records of the Australian Museum.* 41: 47-66.
- . In Press. Aplacophora. In: *Fauna of Australia*. Australian Bureau of Flora and Fauna, Canberra.
- Schwabl, M. 1963. Solenogaster mollusks from southern California. *Pac. Sci.* 17: 261-281.
- Selinka, E. 1885. Report on the Gephyrea collected by H.M.S. Challenger during the years 1873-1876. Report on the Scientific Results . . . of H.M.S. Challenger 13(2): 25 pp.
- Stork, H. A. 1941. Solenogastren der Siboga-Expedition. *Siboga-Exped.* 47b: 45-70. E. J. Brill, Leyden.
- Thiele, J. 1897. Zwei australische Solenogastres. *Zool. Anz.* 20: 398-400.
- . 1902. *Proneomenia amboinensis* n. sp. *Denkschr. Med. nat. ges. Jena* 8: 733-738.
- . 1913. Antarktische Solenogastren. *Dtsch. Südp. Exp.* 14. *Zool.* 6. Heft (1)2: 35-65.
- Turner, R. D. 1985. Notes on the mollusks of deep-sea vents and reducing sediments. *Amer. Mal. Bull. Spec. Ed.* 1: 23-34.

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## PROGRAM AND ABSTRACTS

### 56th ANNUAL MEETING 3-8 June 1990

Marine Biological Laboratory  
Woods Hole, Massachusetts

#### THE APLACOPHORA POSSESS A TRUE RADULAR MEMBRANE

SHELTEMA, Amélie H., Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543 and KUZIRIAN, Alan M., Marine Biological Laboratory, Woods Hole, MA 02543

The radulae of the Aplacophora consist of 6 to more than 40 rows of teeth attached to a membrane. They fall into three categories: distichous, monostichous, and polystichous (two, one, and several teeth per row). Monostichous and polystichous radulae are considered apomorphic based primarily on the fused ducts of their paired salivary glands.

Light and scanning electron microscopic examination of isolated radulae of all three types show the presence of a continuous membranous ribbon to which the teeth are attached. The ribbon and teeth are formed at the blind end of a ventral, pharyngeal radular sac. Thin sections of two species with plesiomorphic distichous radulae reveal actively secreting odontoblasts, membranoblasts, and superior epithelium at the blind end of the sac. The continuous membrane beneath the teeth stains differentially from the attached teeth.

Cellular and hard structures of the aplacophoran radula and radular sac are considered homologous to those in other mollusks because of their similarity in presumed function and topographic positions relative to each other and to the pharynx. The membrane to which the teeth are attached in Aplacophora is thus a true radular membrane and not a part of the pharyngeal cuticle.



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## Abstracts

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### The primitive molluscan radula

The radula in Aplacophora primitively appears to be a paired, non-rasping structure formed of repeated rows of two mirror-image teeth per row. Such a distichous radula is found in the Cambrian fossil *Wiwaxia* and in the early ontogeny of several species of Gastropoda. In some species of Polyplacophora, the radula starts with three, two, or occasionally only one symmetrical pair of mirror-image teeth with the medial one added later. In a number of genera of Aplacophora, the radular membrane itself is divided, that is, paired or bipartite. The polystichous and monostichous radulae found in many other aplacophoran genera are considered to be derived because the ducts of their paired ventral salivary glands are fused. In monostichous radulae, denticles are also fused. The derived radula of the aplacophoran family Prochaetodermatidae has a single unipartite radular membrane bearing distichous hooks and a medial, flat, platelike "rachidian" tooth between them; it is the only aplacophoran radula known to be used for rasping. The observations suggest that the primitive molluscan radula was a paired structure that was not used for rasping.



## Australian Aplacophoran Molluscs: I. Chaetodermomorpha from Bass Strait and the Continental Slope off South-eastern Australia

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**ABSTRACT.** Four new species of Chaetodermatidae (*Chaetoderma usitatum*, *Falcidens chastos*, *F. lipuros* and *F. macrafrondis*) and a new genus and species of Prochaetodermatidae (*Rhabdoderma australe*) are the first Chaetodermomorpha described from off Australia; all are from the shelf in Bass Strait or from the continental slope off southeastern Australia. Two species are numerous: *F. chastos* occurs at densities sometimes up to 180 m<sup>2</sup> from 22 to 120 m in 20 of the 23 shelf samples that contain Chaetodermomorpha, and the prochaetodermatid *R. australe* is common from deeper water, 1,120 to 2,510 m. Several additional species only recently received or with a single specimen are noted but not described; three belong to *Prochaetoderma*, *Limifossor*, or *Scutopus*, thereby extending the recorded ranges of these genera to the western Pacific. Of the 16 species of Chaetodermomorpha collected, four are shelf species occurring at depths of less than 200 m (*F. chastos*, *F. lipuros*, one Prochaetodermatidae, one undetermined), six are upper slope species extending to 1,000 m (three species of *Falcidens*, *Chaetoderma* sp., *Scutopus* sp., *Limifossor* sp.) and six extend below 1,000 m (*C. usitatum*, *F. macrafrondis*, *R. australe*, *Falcidens* sp., *Chaetoderma* sp., *Prochaetoderma* sp.). These depth distributions are similar to other Pacific Chaetodermomorpha genera except for *Chaetoderma*, a genus usually common on the shelf but missing from Bass Strait.

SCHELTEMA, A.H., 1989. Australian Aplacophoran Molluscs: I. Chaetodermomorpha from Bass Strait and the Continental Slope off south-eastern Australia. Records of the Australian Museum 41(1): 43-62.

Aplacophoran molluscs belonging to the footless, burrowing group comprising the subclass Chaetodermomorpha (= Caudofoveata) have not been reported before from off Australia. Five species in two families and three genera are described here from recent collections made on the slope off southeastern Australia and the shelf in Bass Strait.

### Materials

A total of 231 specimens in 27 samples were examined: 23 samples were taken between 22 and 130 m in Bass Strait,

three samples from the continental slope off south-east Victoria between 1,120 and 2,510 m, and one sample from 1,200 m off Wollongong, New South Wales (Table 1). Twenty five of the Bass Strait stations are part of the Museum of Victoria Bass Strait Survey (RV *Hai-Kung*, FV *Sarda*, RV *Tangaroa*); one sample from the Bass Strait (Esso-Gipps Stn 20) and one sample from off Wollongong (FRV *Kapala*) comprise part of the collection of the Australian Museum (AMC149631 and AMC149638, respectively). In addition, 937 specimens from 17 stations taken by the Museum of Victoria between 363 and 1,850 m on the slope off Point Hicks (RV *Franklin*) have been

recently received and cursorily examined; a few data from these stations are included here (slope stations 25 and 27, Table 1; Discussion).

### Methods

Descriptions of Chaetodermomorpha are based on external morphology, including measurements of body divisions, shape of oral shield, and attitude of spicules on the body wall; morphology of spicules; and morphology of entire, isolated radulae (see Scheltema, 1976, 1985, for more complete accounts of descriptive and statistical methods). Measurements of specimens were made with dividers on lines drawn lengthwise and crosswise on microscope images using a camera lucida attached to a dissecting microscope. The oral shield index is calculated by  $[(\text{length} \times \text{width}) \div \text{greatest trunk diameter} \times 100]$ .

Spicules were removed by teasing after placing the specimen in a drop of glycerine in a depression slide; drawings were made using a camera lucida. Thickness was

determined by using cross-polarised light, and lines were drawn between selected colour bands, or isochromes (Scheltema, 1985). Figure 1A shows morphological characters of a spicule.

Radulae were isolated by dissecting out the buccal mass and removing the tissue with sodium hypochlorite in a depression slide; after thorough rinsing, a drop of glycerine was added. Small radulae were removed in a drop of glycerine to a flat slide and examined under a coverslip.

Permanent slides were made of spicules from the holotype and of spicules and radulae from paratypes. Spicules were teased directly onto a slide and air-dried before mounting in a standard histologic mountant. Radulae were retrieved from the glycerine preparation, washed in distilled water in a depression slide, and run through a dehydration series before mounting.

Scanning electron microscope photographs were taken of holotype spicules using a JEOL JSM-840 microscope (Fig. 2).

Types and paratypes are deposited in either the Museum of Victoria, Melbourne (MV) or the Australian Museum.

Table 1. Specimens examined. C.u. = *Chaetoderma usitatum*; F.C. = *Falcidens chistos*; F.I. = *Falcidens lipuros*; F.m. = *Falcidens macrafrondis*; R.a. = *Rhabdoderma australe*; P.sp. = *Prochaetoderma* sp.; Sp.undet. = Species undetermined.

Cruise <sup>1</sup> and Stn	Gear <sup>2</sup>	Date	Depth m	Lat. S	Long. E	Sediment <sup>3</sup>	C.u.	F.C.	F.I.	F.m.	R.a.	P.sp	Sp.undet
Sa80-113	S-M	3/11/80	66	40°23.9'	145°32'	msh		1					
HK-139	T	7/2/81	55	40°43.8'	148°32.7'	s							1
T-155	ES	12/11/81	70	38°56.0'	145°16.6'	m		12					
T-155	S-M	12/11/81	70	38°55.5'	145°17.0'	m		9					
T-156	ES	13/11/81	74	39°45.9'	145°33.5'	m		13					
T-156	S-M	13/11/81	74	39°45.9'	145°33.3'	m		18					
T-157	ES	13/11/81	75	40°10.9'	145°44.3'	m		7					
T-157	S-M	13/11/81	75	40°10.9'	145°44.3'	m		1					
T-158	ES	13/11/81	82	39°48.6'	146°18.8'	m		38					
*T-159	ES	13/11/81	80	*39°46.0'	*146°18.0'	m		*64					
T-159	S-M	13/11/81	80	39°43.5'	146°18.8'	m		7					
T-163	ES	14/11/81	56	43°43.9'	148°32.5'	ms		1					
T-163	S-M	14/11/81	56	43°43.9'	148°32.5'	ms							1
T-165	ES	14/11/81	60	40°13.8'	148°39.6'	ms		1					
T-165	S-M	14/11/81	60	40°14.4'	148°30.0'	ms		1					
T-166	S-M	14/11/81	22	40°06.8'	148°24.4'	sh		1					
T-169	ES	15/11/81	120	39°02.4'	148°30.6'	sm		4		1			
*T-170	S-M	15/11/81	130	*38°57.8'	*148°26.5'	ms				*2			
T-179	ES	18/11/81	55	39°03.2'	146°39.5'	ms		1					
T-180	ES	18/11/81	65	39°12.9'	146°27.3'	ms		1					
T-181	ES	19/11/81	79	38°39.8'	144°18.2'	fs		3					
T-181	S-M	19/11/81	79	38°39.8'	144°18.2'	fs		10					
T-Q631	P	15/11/81	1120	38°35.1'	148°36.8'	sm					1	1	1
T-Q634	P	16/11/81	2510	38°42.3'	148°48.0'	m					1		
T-Q635	P	16/11/81	1730	38°55.6'	148°46.4'	scl					6		
E-G 20	n.d.	5/69	95	39°00.0'	148°24.8'	s		6					
*K76-23-02	n.d.	13/12/76	1200	*34°27.26'	*151°27'	n.d.	*6			*2	*9		
F-Slope 25	ES	22/7/86	1850	38°25.9'	148°58.6'	m	1				5		
F-Slope 27	ES	22/7/86	1500	38°26.0'	149°00.0'	cl	6				47	4	
Totals							13	199	3	2	69	5	3

<sup>1</sup> Sa80 = F.V. *Sarda*, Nov. 1980; HK = RV *Hai-Kung*, Feb. 1981; T = RV *Tangaroa*, Nov. 1981; E-G = *Esso-Gipps*, May 1969; K76 = FRV *Kapala*, Dec. 1976; F = RV *Franklin*, July 1986.

<sup>2</sup> S-M = Smith-MacIntyre grab, 0.1 m<sup>2</sup>; ES = epibenthic sled; P = pipe dredge; T = trawl.

<sup>3</sup> cl = clay; fs = fine sand; m = mud; ms = muddy sand; msh = muddy shell sand; s = sand; scl = silty clay; sh = shell; sm = sandy mud.

\* Type locality

Sydney (AM).

## Systematics

### Chaetodermomorpha Pelseneer, 1905

Chaetodermomorpha Pelseneer, 1905  
Caudofoveata Boettger, 1956

**Diagnosis.** Aplacophora lacking ventral furrow and foot; with oral shield as extension of pharyngeal cuticle (Scheltema, 1981, 1988) and with paired gills in cloaca (mantle cavity); often with distinct narrow constriction anteriorly; stomach and digestive gland differentiated from each other (Scheltema, 1981); radula distichous with bipartite or fused (unipartite) radular membrane (Scheltema, 1981,

1988), or radula specialised into a cone with a pair of denticles (Scheltema, 1972); spicules solid and more or less leaf-shaped, with distinct or indistinct dorsoterminal sensory organ (Haszprunar, 1987)

### Chaetodermatidae Manon, 1885

**Diagnosis.** Chaetodermomorpha having a cone-shaped radula with a pair of denticles, arrangement of internal organs and musculature reflected externally by 4 body divisions: neck, anterior trunk, posterior trunk, and posternum, which vary among species in length relative to total body length; anterior constriction between neck and anterior trunk usually obvious (Figs 3, 10).

### Chaetoderma Lovén, 1844

Chaetoderma Lovén, 1844

Crystallophrisson Möbius, 1875 (Ivanov, 1981. (See Heppell, 1963, Bulletin of Zoological Nomenclature, 1966, Opn 764, Salvini-Plawen, 1984)

**Type species.** *Chaetoderma nitidulum* Lovén, 1844, by monotypy.

**Diagnosis.** With characters of the family. Radula with paired denticles lying outside dome-shaped membrane which covers the buccal mass and with paired lateral projections extending from radula cone to dome-shaped membrane opposite base of denticles (Fig. 5).

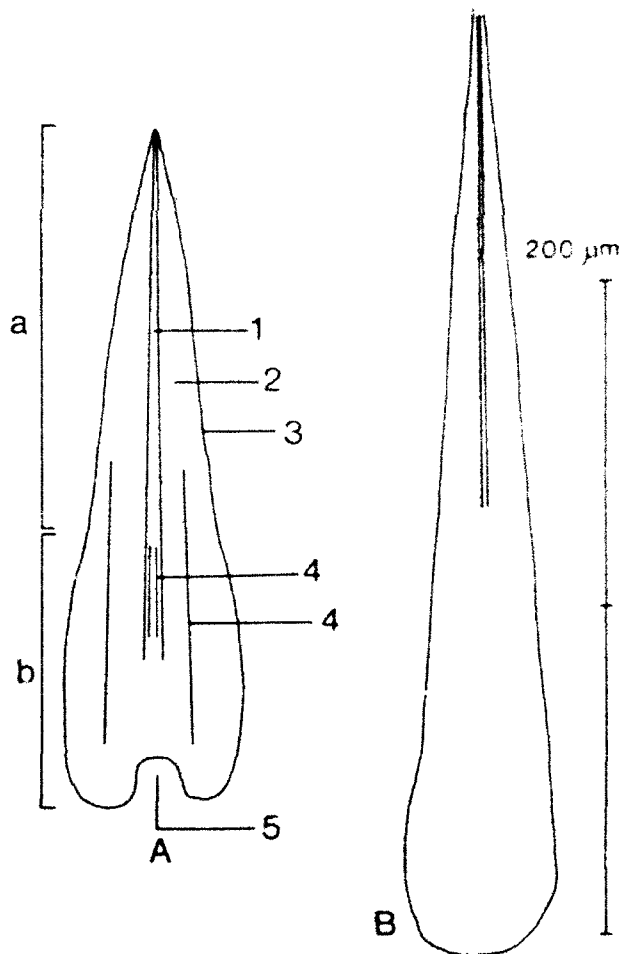
**Distribution.** World ocean except Antarctic, especially near coasts.

### *Chaetoderma usitatum* n.sp.

Figs 2A, 2B, 3, 4, 5; Table 1

**Type material.** HOLOTYPE, off Wollongong, NSW, 34°27'26"S, 151°27'E, 1,200 m. AM C156232 (wet specimen, spicule slide. Second spicule slide MV F54194). PARATYPES 1, 2: type locality. AM C156233 (1), C156234 (2)

**Diagnosis.** Large, up to nearly 3 cm in length, posterior trunk half or less total length, up to about 2 mm in diameter, longer and wider than anterior trunk; spicules up to 400 µm long, greater than 100 µm thick in all body regions, thickest medially with broad keel, flared base, distinct waist, and narrow blade, those of neck and anterior trunk bent outwards and held perpendicular to body wall with sediment densely packed between them, those of posterior trunk flat lying; radula large, up to 550 µm in total length and two fifths neck diameter, lateral projections short, 40-60 µm, dome-shaped membrane extending one third distance along



**Fig.1.** A: Generalised spicule, distal end at top, showing morphology: 1, medial keel; 2, isochrome (line between two color bands) as seen under cross-polarised light; 3, side edge; 4, ridges; 5, basal notch; a, blade; b, base; the waist lies between a and b. Spicule length is the distance between most proximal and most distal points; width of blade and of base is the greatest distance between their side edges. B: Spicule of *Prochaetoderma* sp. from Sin Q631 (see Table 1); greatest thickness 9 µm

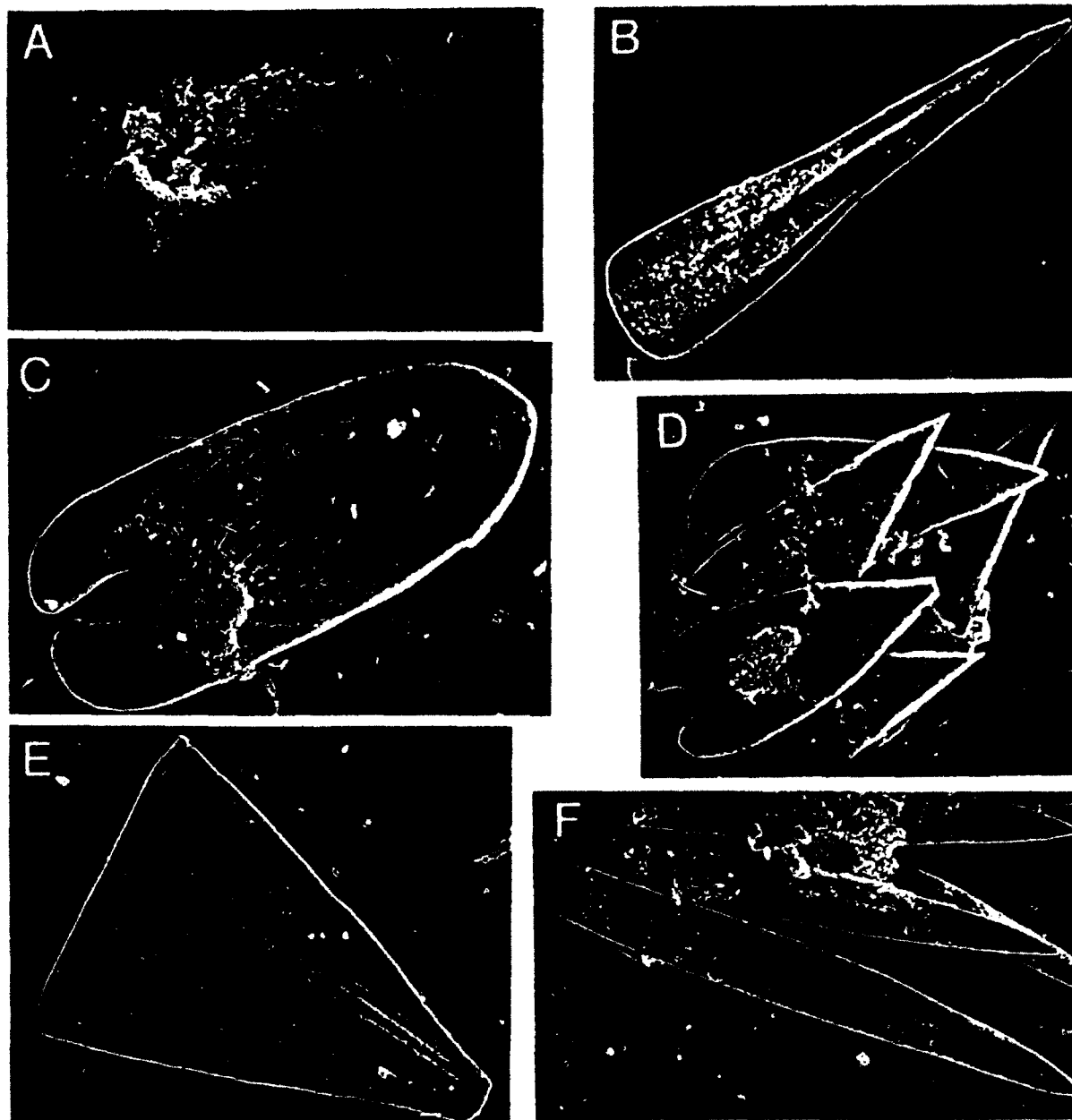
cone, cone nearly square in cross-section, 150 by 190  $\mu\text{m}$ , denticles about 50  $\mu\text{m}$ .

**Etymology.** From *usitatum*, meaning usual.

**Description.** *External morphology.* *Chaetoderma usitatum* is largest Chaetodermomorpha in samples from off south-east Australia ranging up to nearly 3 cm in length (Fig. 3); smallest specimen in collection measures 7.1 mm. Body conforms to a shape common for genus

*Chaetoderma*. Neck is short, one tenth body length, anterior trunk shorter than posterior trunk, which is one half or less body length; posterium less than one tenth body length. Anterior trunk widest at usually distinct anterior constriction. Neck and anterior trunk about same diameter, up to 1.5 mm; diameter of posterior trunk nearly one and one half times that of greatest anterior trunk diameter and measures up to 1.9 mm.

Spicules of neck and anterior trunk held perpendicular to body wall and are scarcely visible because of sediment



**Fig. 2.** Spicules from holotypes of: A: *Chaetoderma usitatum* n.sp., body region 'e' (see Fig. 4). B: *C. usitatum*, region 'g'; C: *Falcidens chiastos* n. sp., region 'e' (see Fig. 7); D: *Falcidens lipuros* n.sp., between regions 'd' and 'e' (see Fig. 11); E: *Falcidens macrofrondis* n.sp., distal half of large trunk spicule (see Figs 13A, 14); F: *Rhabdoderma australe* n.sp., body region 'c' (see Fig. 16), showing fine longitudinal striations. Scale bars = 50  $\mu\text{m}$

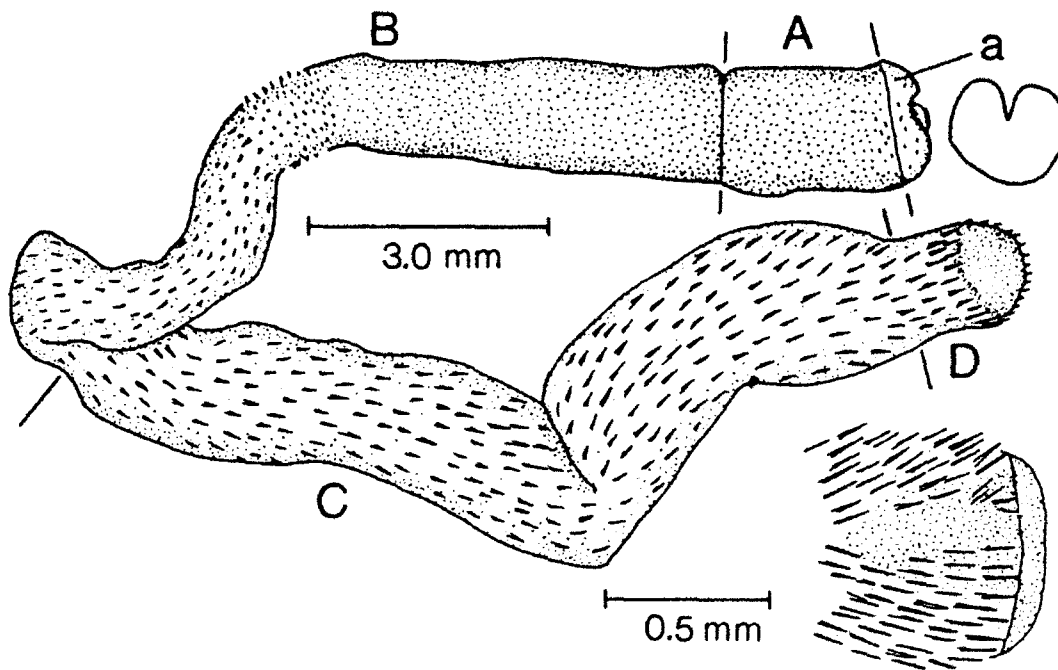


Fig. 3. *Chaetoderma usitatum* n.sp., holotype, with oral shield and posterium/cloaca shown enlarged. Coarse stippling indicates sediment packed between the spicules; sediment perhaps covers the dorsoterminal sensory organ of the posterium, which is drawn in dorsal view. Body divisions are a, anterium; A, neck; B, anterior trunk; C, posterior trunk; D, posterium.

packed between them from distal tips to cuticle. Spicules of posterior trunk flat lying and easily dislodged, leaving body translucent where they are missing.

Anterium and oral shield usually exposed; oral shield of moderate size for genus and has short dorsal cleft.

Cloaca flattened on posterior end and packed with sediment; spicules of cloaca not noticeably longer than those of posterium and do not form discrete ring. Dorsoterminal sensory organ not evident, probably hidden by sediment.

**Holotype:** total length 26.3 mm; anterium 0.3 mm long; neck 2.1 mm long by 1.4 mm in diameter; anterior trunk, which is stretched beyond natural condition, is 11.5 mm long by 1.3 mm in diameter; posterior trunk 11.2 by 1.9 mm; posterium 1.2 by 0.7 mm; oral shield is 0.35 mm in width by 0.30 mm in height; index 5.53.

**Spicules.** Spicules from all body regions thickest medially, greater than 10  $\mu\text{m}$ , with usually broad, flared base, distinct waist, relatively narrow blade with distinct, broad keel (Figs 2A and B, 4). Lengths increase from about 100  $\mu\text{m}$  on neck (region 'b') to about 400  $\mu\text{m}$  on posterior part of posterior trunk (region 'h'). Spicules from neck and anterior part of anterior trunk (regions 'b'-'d') are bent outward at a 20-30° angle; those from posterior part of anterior trunk are less bent (region 'e'); and those from posterior trunk (regions 'f'-'h') are nearly flat, slightly bent toward body. Thickest part of spicule shifts from base in spicules from anterium, neck and most anterior trunk (regions 'a', 'b', 'c') to waist in spicules from trunk regions 'e'-'h' and back to proximal end on spicules from posterium (region 'i'). Base and blade are of about equal length on bent spicules from neck and anterior trunk ('b'-'e'); blade

becomes relatively longer on nearly flat spicules of posterior trunk ('f'-'h'). Base widths of bent trunk spicules ('c', 'd') more than 2 to 3 times blade width and bases flared, i.e., widest part proximal. In spicules of neck ('b'), midtrunk ('e') and posterior trunk ('f'-'h'), base width 2 times blade width or less. Two types of spicules predominate in mid- and posterior trunk regions ('e'-'h'): in one, edges of base flared; in other, edges of base nearly parallel. Blades of latter type narrower than those of former. Third type of spicule found scattered throughout trunk, short, with edges of base and blade very convex and blade wide relative to base.

Besides keel, ornamentation restricted to ridge parallel to each edge from below waist to midblade; a few short ridges are present on keel of some spicules from mid- and posterior trunk ('e'-'h').

Spicules of posterium ('i') long (more than 300  $\mu\text{m}$ ), narrow (less than 50  $\mu\text{m}$ ), without waist, bluntly pointed; some short, thin, sharply keeled, asymmetric spicules with one edge more curved than other, tapered proximally, also present.

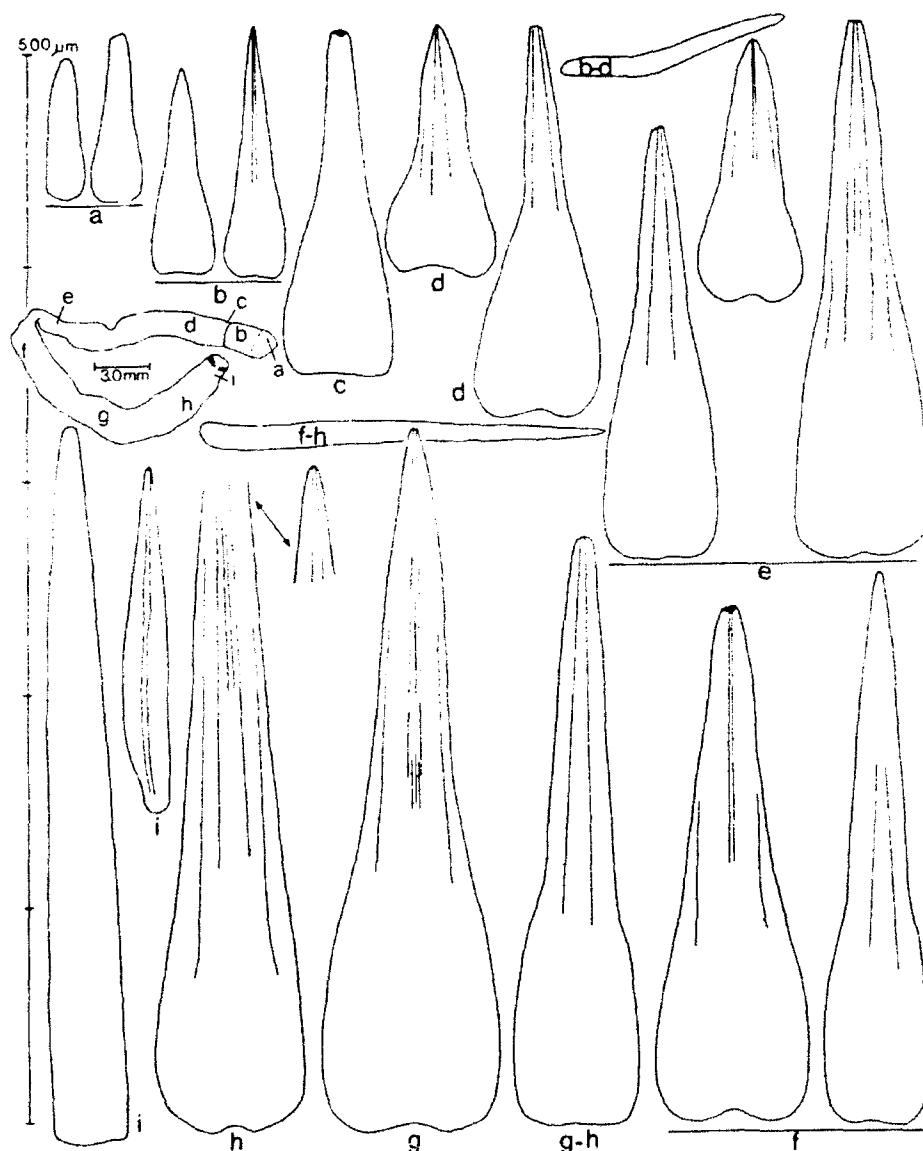
**Radula.** Two radulae were examined (Fig. 5). Radula large, 500 and 550  $\mu\text{m}$  in total length, nearly two fifths neck diameter. Cone of one radula is 470  $\mu\text{m}$  long and nearly square in cross-section, 150  $\mu\text{m}$  wide on anterior and posterior sides and 190  $\mu\text{m}$  laterally (see description of radula under *Falcidens chistos* below for orientation). Lateral projections very short, 40 to about 60  $\mu\text{m}$ . Dome-shaped membrane (200 and 275  $\mu\text{m}$ ) extends about one third of distance along cone. Denticles, seen clearly in only one radula, are 52  $\mu\text{m}$ .

**Distribution.** The species is known from 13 specimens taken between 1,200 and 1,850 m off Point Hicks, Victoria, and off Wollongong, New South Wales (Table 1).

**Closely related species.** *Chaetoderma californicum* Heath, 1911 is a north-eastern Pacific species taken from between 1100 and 1200 m off San Diego, California (holotype, known only from slides) and from 800 m (1 specimen) and 1600 m (2 specimens) off the coast of Oregon. (The holotype slides and Oregon specimens have been examined but a redescription of the species has not yet been published.). *Chaetoderma californicum* is similar to *C. usitatum* in general body shape and size, in morphology of the posterior trunk spicules, and in size of the radula. However, the anterior trunk spicules of *C. usitatum* have a longer and narrower blade than those of *C. californicum*,

the neck is shorter relative to total body length, and the oral shield is smaller. In *C. californicum* the ratio of posterior to anterior trunk width (2 times) is greater than in *C. usitatum* (1.5 times) and the length of the lateral projection of the radula is up to 2 times greater.

*Chaetoderma sibogae* (Stork, 1941) [= *C. indicum* (Stork)] from 959 and 1,886 m in the Java Sea is similar in body shape, and the posterior part of the anterior trunk is similarly distorted by stretching, but the species is too poorly described for a more precise comparison. *Chaetoderma akkesiensis* Okuda, 1943 from 54 m off Japan is likewise similar in shape, but the illustrated spicules are dissimilar, as are those of *Chaetoderma militare* Selenka, 1885 from the Philippines (genus of the latter is uncertain, and the species is poorly described).



**Fig.4.** Spicules of *Chaetoderma usitatum* n.sp., paratype no. 1 (illustrated at middle left), from the anterior ('a'), neck ('b'), anterior trunk ('c'-'e'), posterior trunk ('f'-'h'), and posterior ('i'). Side views are labelled 'b'-'d' and 'f'-'h'; distal end is to the right, outer surface is above. Greatest thickness is greater than 10  $\mu$ m for all body regions, but most from the anterior ('a') are 10  $\mu$ m or less.

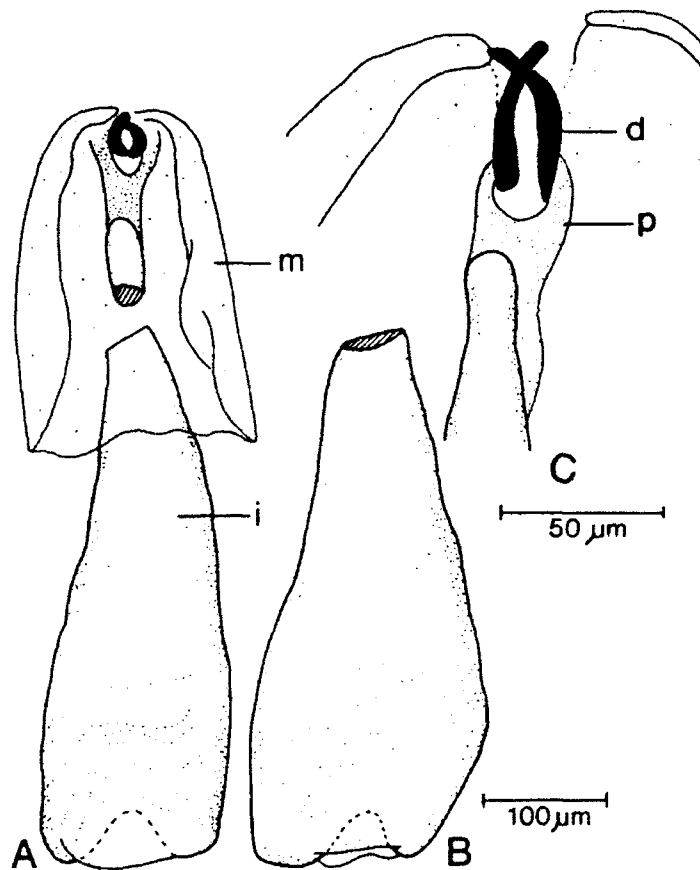


Fig. 5. Radula of *Chaetoderma usitatum* n.sp. A, B: paratype no. 1, cone broken: A, posterior view; B, lateral view; C: paratype no. 2 showing detail of lateral projections. d, denticle; i, cone-shaped piece; m, dome-shaped membrane which covers buccal mass; p, lateral projection.

***Falcidens* Salvini-Plawen, 1969**

*Falcidens* Salvini-Plawen, 1969.

*Chaetoderma*.-Ivanov, 1981 (non Lovén, 1844). (See Salvini-Plawen, 1984).

**Type species.** *Falcidens crossotus* Salvini-Plawen, 1984, by original designation.

**Diagnosis.** With characters of the family. Radula with paired sickle-like teeth attached to the cone-shaped piece (Figs 9, 12, 13).

**Distribution.** World ocean except Antarctic, especially near coasts.

***Falcidens chistos* n.sp.**

Figs 2C, 6, 7, 8, 9; Table 1

**Type material.** HOLOTYPE: Bass Strait, 39°46.0'S, 146°18.0'E, 80 m (RV *Tangaroa*, Stn 159 epibenthic sled, 13 Nov. 1981). MV F54192 (wet specimen, spicule slide. Second spicule slide AM). ILLUSTRATED PARATYPES: Nos 1, 2, 4: type locality. MV F54190

(no.1), F54189 (no. 2) and F54191 (no.4). No. 3: Bass Strait, 39°00'S, 148°24'50"E, 95 m (Esso-Gipps Stn 20, May 1969). AM C156227.

**Diagnosis.** Translucent and shiny, slender, up to 12 mm long by 0.8 mm diameter, anterior trunk short, narrower than posterior trunk which is about half total body length, anterior constriction not pronounced, posterium less than one quarter body length; spicules mostly flat lying but somewhat erect on anterior trunk and posterium, without distinct waist, ornamented by crossed diagonal ridges, with 25 µm notch or rounded basally, about 50 µm in width, ranging up to 150 µm in length, thickness 8 µm or less; radula length up to 220 µm, cone-shaped piece narrow anteriorly, 10-20 µm, and broad laterally, 60 µm or more, sickle teeth 35 µm, distal ends set widely apart, lateral membranes long, extending one half length of cone.

**Etymology.** From *chistos*, arranged diagonally.

**Description.** *External morphology.* Slender, translucent species up to 12 mm in length (Fig. 6). About 50 percent of body length occupied by posterior trunk containing digestive gland and gonad (range, 38-60 percent, N = 49,

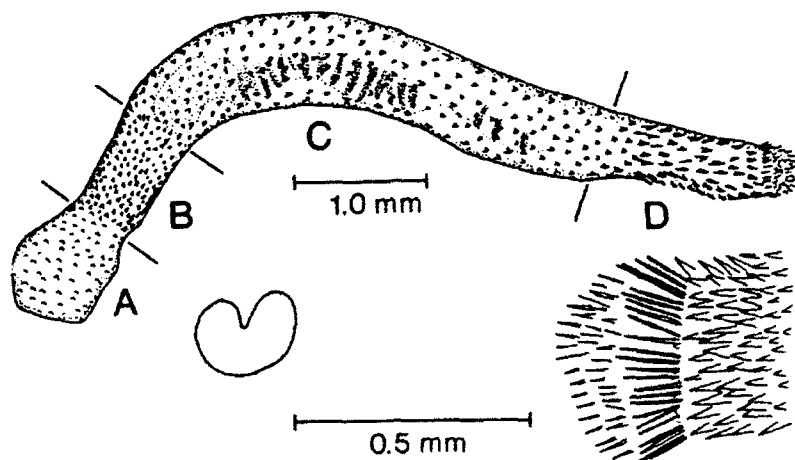


Fig.6. *Falcidens chiastos* n.sp., holotype, entire specimen and cloaca in lateral view, and oral shield of paratype no. 4. Spicules of cloacal region are heavily encrusted, not indicated here. Body divisions are A, neck; B, anterior trunk; C, posterior trunk; and D, posteriorium.

Stn 159 ES); anterior trunk and posteriorium short relative to total length, averaging 14 and 23 percent, respectively (ranges, 9-23 percent and 16-30 percent, respectively). Neck about same length as anterior trunk, but of greater diameter (mean diameters 0.6 and 0.4 mm, respectively); constriction between them not pronounced. Long posterior trunk somewhat broader than anterior trunk, averaging 0.6 mm. Narrowest region is the posteriorium (0.3 mm average).

Spicules on neck and posterior trunk flat lying; internal organs visible, especially dark-coloured stomach and folds of digestive gland. Anterior trunk and posteriorium opaque, spicules somewhat erect in preserved specimens. Cloaca ringed by short circle of spicules and bears a brush of usually heavily encrusted needles. Dorsoterminal sensory organ not evident.

Oral shield only slightly wider than high and cleft dorsally; withdrawn in most specimens. Dimensions in paratype no. 4 are 0.16 mm in height by 0.21 mm in width; index is 4.20.

**Holotype:** total length 6.6 mm; neck 0.9 long by 0.7 mm in diameter; anterior trunk 0.8 by 0.5 mm; posterior trunk 3.6 by 0.7 mm; posteriorium 1.3 by 0.3 mm.

**Spicules.** Crossed diagonal ridges ornamenting spicules at indistinct waist give species its name (Figs 2C, 7). Most spicules about 50  $\mu$ m in width, symmetrical and curved slightly toward body; thickest, 6-8  $\mu$ m, where diagonal ridges cross. Spicules of neck ('b') ovate or widest distally and less than 75  $\mu$ m in length; those from anterior and posterior trunk ('c'-f) and posteriorium ('g') 100-150  $\mu$ m, at least twice as long as wide. Spicules from neck and trunk rounded distally or rounded with a broad point; those from posteriorium have a broad point. Proximally, spicules either notched deeply (notch about 25  $\mu$ m long) or unnotched; neither type predominates. Unnotched spicules either

rounded or straight basally. Notch openings vary in width of gap from nearly closed (less than 2  $\mu$ m) to more than notch width (greater than 10  $\mu$ m) (Fig. 8). Spicules from region near cloaca ('h') vary from broad and short (50 by 10  $\mu$ m) with short, sharp distal point to narrow and long (35  $\mu$ m or less by 125-175  $\mu$ m) with a long distal point. Needle-like spicules of 150  $\mu$ m also occur at cloaca.

**Radula.** Three radulae examined, ranging in total length from 185-220  $\mu$ m, one quarter to more than one third neck diameter (Fig. 9). Radula in preserved specimens of *Falcidens* oriented with sickle teeth dorsal; largest, and growing, end of cone ventral; and triangular plate faces anteriorly. (Triangular plate probably not attached to sickle teeth as described by Scheltema [1972], but may instead be a guide against which ride the sickle teeth, which are attached to the cone [cf. Fig. 9C and F]). Cone-shaped piece ('i') very narrow anteriorly and posteriorly (12-24  $\mu$ m) and 3-5 times broader laterally, 60  $\mu$ m or more at greatest width; cone length in figured paratypes 165 and 185  $\mu$ m. Sickle teeth ('h') are about 35  $\mu$ m from base to tip and gape broadly at tips. Entire triangular plate ('c') tanned (i.e., yellowed); has ridges along outer edges (Fig. 9E). Apophyses of triangular plate consist of a bar-shaped piece ('b') and two denticles ('a'). Pair of thin lateral membranes ('y') that lie outside buccal mass about 105  $\mu$ m long and extend almost half length of cone.

**Distribution.** *Falcidens chiastos* is the most numerous Chaetodermomorpha species in the Australian samples (Table 1). A total of 199 specimens were examined, all from Bass Strait between 22 and 120 m; sediments ranged from fine muds to fine sands and shell. Densities at some stations were high: 180 m<sup>2</sup> at Stn 156 S-M, 100 m<sup>2</sup> at 181 S-M, and 70 m<sup>2</sup> at 151 S-M.

**Closely related species.** *Falcidens loveni* (Nierstrasz, 1902), described from two complete specimens and a



fragment dredged on the *Siboga* expedition from 1,310 m in the Java Sea (8°0.3'S, 116°59'E, Stn 35), has spicules with similar diagonally crossed ridges (Fig. 7) and a similar body shape. *Falcidens chistos* differs from *F. loveni* as illustrated by Nierstrasz, however, in having a significantly shorter posterium relative to total length ( $p$  less than 0.01 in one population, Stn 159 ES; see Scheltema, 1985, for statistical importance of relative posterium length between species). The spicules of *F. chistos* are broader relative to their length and more deeply notched than those illustrated for *F. loveni*. The sickle teeth of the radula differ in the two species (Fig. 9); in *F. chistos*, they have a shorter proximal

base and a wider gap between the distal ends than in the illustration for *F. loveni*.

A *Falcidens* species similar to *F. chistos* occurs between 400 and 600 m on the slope off south-eastern Victoria. A preliminary examination shows it to have longer and narrower spicules with the diagonal ridges incomplete or lacking and with a shallower basal notch.

Two other unnamed species of *Falcidens* with similar notched spicules ornamented by crossed diagonal ridges occurs in the western Atlantic off south-eastern United States and north-eastern South America.

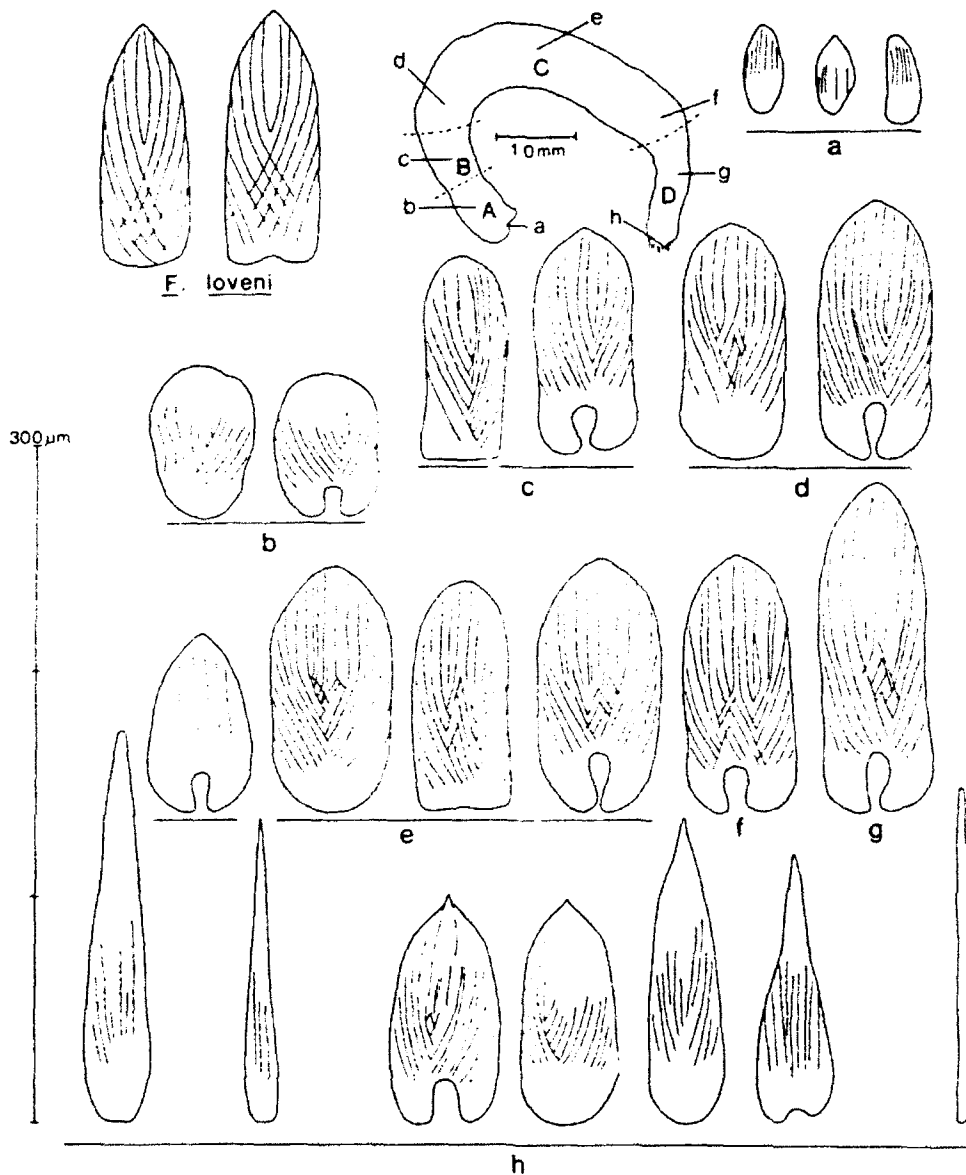
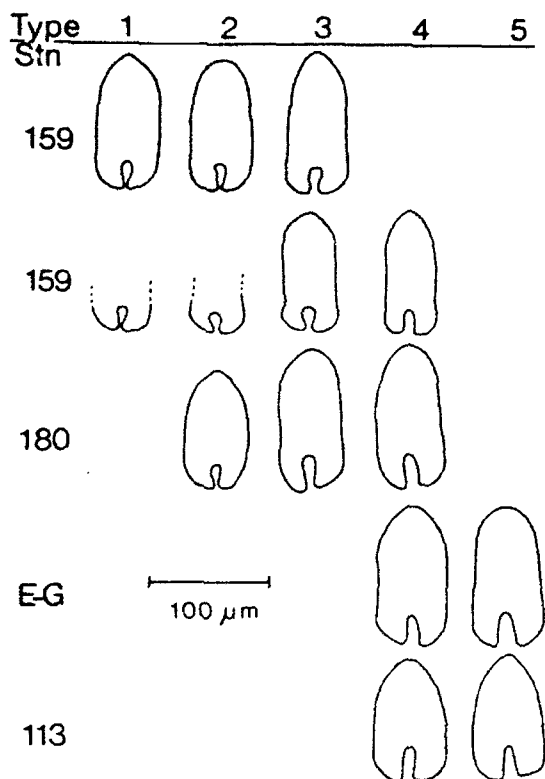


Fig. 7. Spicules of *Falcidens loveni* Nierstrasz and *F. chistos* n.sp. Spicules of *F. loveni* at upper left are redrawn from Nierstrasz (1902, Fig. 183) (scale unknown). 'a'-'h', spicules of *F. chistos* from paratype no. 1 figured at top: 'a', from oral region; 'b', from neck; 'c', from anterior trunk; 'd', 'e', 'f', from anterior, midpart, and posterior part of posterior trunk; 'g', from posterium; 'h', from around cloaca. Greatest thicknesses for body regions are: 'a', less than 3 μm; 'b', 6.5 μm; 'c'-'f', 8 μm; 'g', 7.5 μm; 'h', 7 μm.



**Fig. 8.** *Falcidens chiastos* spicules, variation in notch width at proximal end of spicule. Spicules in each horizontal row are from the midposterior trunk of a single specimen from the location indicated by station number or letter (see Table 1). Vertical rows show type of spicule notch: 1, nearly closed proximally, opening less than 2  $\mu\text{m}$ ; 2, somewhat open, opening 2 to less than 5  $\mu\text{m}$ ; 3, width of opening broad but less than greatest notch width, 5–7  $\mu\text{m}$ ; 4, notch of even width, sides of notch nearly parallel, opening 8–10  $\mu\text{m}$ ; 5, notch widest at opening, greater than 10  $\mu\text{m}$ .

*Falcidens lipuros* n.sp.

Figs 2D, 10, 11, 12; Table 1

**Type material.** HOLOTYPE: Bass Strait, 38°57.8'S, 148°26.5'E, 130 m (RV *Tangaroa*, Stn 170 Smith-McIntyre grab, 15 Nov 1981). MV F54188 (wet specimen, spicule slide. Second spicule slide AM). ILLUSTRATED PARATYPE: No. 1: type locality. MV F54187.

**Diagnosis.** Short, thick body up to 6.7 mm long, broadest at anterior trunk (up to 1.0 mm in diameter), tapered posteriorly, posteriormore short and not tail like, posterior trunk more than half total body length, anterior constriction narrow but distinct; trunk spicules flat lying, elongate, up to 200  $\mu\text{m}$  long and 50  $\mu\text{m}$  wide, less than 8  $\mu\text{m}$  thick, notched or rounded basally, many with broad ridges at waist not parallel to edges or medial axis, waist usually distinct, blade pointed distally; radula 200  $\mu\text{m}$  long, cone narrow anteriorly, 15  $\mu\text{m}$ , and broad laterally, 60  $\mu\text{m}$ .

sickle teeth 48  $\mu\text{m}$  with points nearly meeting, lateral membranes short, extending less than one quarter length of cone.

**Etymology.** From *lipuros*, without a tail.

**Description.** *External morphology.* Short, anteriorly broad species without distinct tail, or posteriormore (Fig. 10). Greatest length of 3 known specimens 6.7 mm. Anterior trunk short, only one sixth total length, and broadest part of body, up to 1.0 mm in diameter. Neck short, one tenth body length, 0.1–0.2 mm narrower than anterior trunk; very narrow but distinct constriction appears as fine line between them. Posterior trunk more than half total length; tapers gradually to posteriormore, narrowing to 0.1 or 0.2 mm less in diameter than anterior trunk. Short posteriormore, one sixth total length, is relatively broad, 0.4–0.5 mm in diameter. Anterior and posterior ends of body flat when contracted. Dorsoterminalsensory organ evident. Oral shield of paratype no. 1 twice as wide laterally as high (0.27 by 0.14 mm), with deep dorsal cleft extending more than halfway ventrally; index is 4.72.

Spicules flat lying and distinctly pointed; increase in length posteriorly. Posterior trunk translucent, dark digestive gland apparent. Cloaca encircled by a ring of spicules shorter than those of posteriormore; spicules of contracted posterior wall converge like spokes of a wheel into center.

**Holotype:** total length, 6.8 mm; neck 0.8 long by 0.8 mm diameter; anterior trunk 0.9 mm by 1.0 mm; posterior trunk 4.2 by 0.9–0.8 mm posteriorly; posteriormore 0.9 by 0.5 mm.

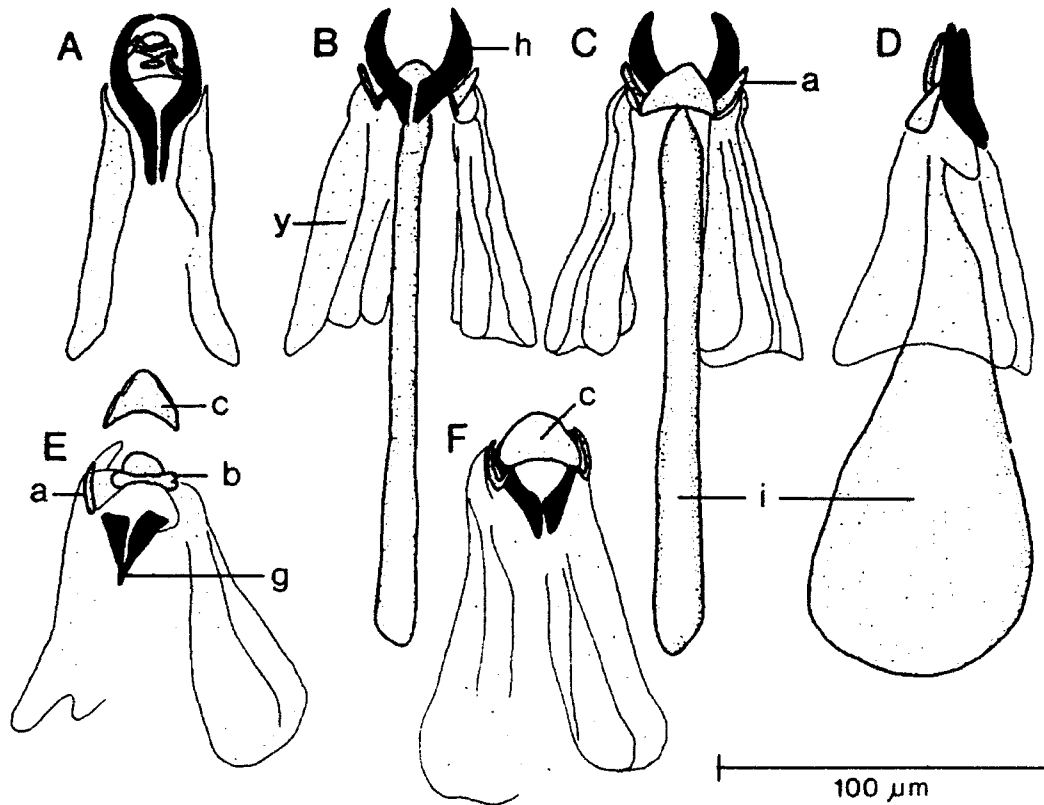
**Spicules.** Spicules of *F. lipuros* symmetrical, flat and either notched or rounded basally (Figs 2D, 11). Side edges of both base and blade convex; waist usually distinct (but indistinct in Fig. 2D); many, but not all, spicules have distinct, wide, longitudinal grooves and ridges at waist not parallel to sides or to medial axis. Thickest part of spicules is medial and extends from base to just beyond waist; greatest thickness (up to 8  $\mu\text{m}$ ) same in neck and trunk spicules. Blade broad relative to base. Distal tips thin and often broken off.

Spicules from oral region ('a') thin (up to 4  $\mu\text{m}$ ), elongate (up to 60  $\mu\text{m}$  long by 20  $\mu\text{m}$  wide), often somewhat pointed, without ridges. Spicules of neck ('b') and anterior trunk ('c') have broad blade with distinctly convex edges, end in a nipple-like point distally. Blades and bases about equal in length; total lengths and base widths range up to 100 by 42  $\mu\text{m}$  on the neck and up to 120 by 50  $\mu\text{m}$  on anterior trunk.

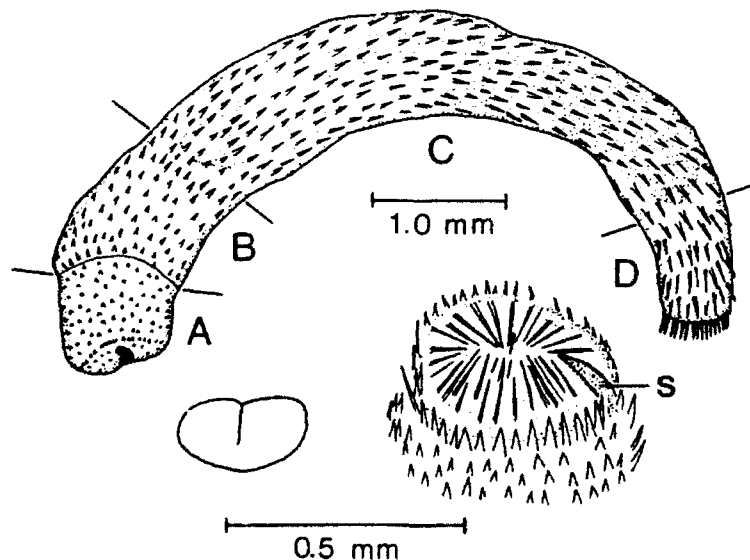
Blades in spicules of posterior trunk ('d', 'e') longer than bases, have only slightly convex edges, ending in a point not set off from rest of blade. Spicule lengths and base widths range up to 180 by 50  $\mu\text{m}$  anteriorly and up to 200 by 55  $\mu\text{m}$  posteriorly.

Spicules of posteriormore ('f') have elongate, narrow blades and range up to 350  $\mu\text{m}$  in length, 50  $\mu\text{m}$  in width, and 10  $\mu\text{m}$  in thickness; interspersed are spicules like those of trunk.

Scattered on neck and trunk are few thin (4–5  $\mu\text{m}$ ), short,



**Fig.9.** Radula of *Falcidens loveni* (Nierstrasz) (A) and *F. chiastos* n.sp. (B-F). A: redrawn from Nierstrasz (1902, fig.191); B-D: paratype no. 1, posterior (B), anterior (C), and lateral (D) views; E: paratype no. 2; F: paratype no. 3. In E, the triangular plate 'c' has broken away from its apophyses 'a' and 'b' and shows ridged edges; the sickle teeth 'h' are broken off, but the proximal spring connection 'g' remains. In F the triangular plate 'c' is more distal relative to the sickle teeth than in the radula drawn in B and C, probably indicating preservation at different times of radula movement. a, b, apophyses of triangular plate; c, triangular plate; g, spring-like connection of sickle teeth; h, sickle teeth; i, cone-shaped piece; y, lateral membranes that lie outside buccal mass. Scale applies to B-F; unknown for A.



**Fig.10.** *Falcidens lipuros* n.sp., holotype. entire specimen and posterolateral view of cloaca, and oral shield of paratype no. 1. Body divisions are A, neck; B, anterior trunk; C, posterior trunk; and D, posterior. The dorsoterminal sensory organ ('s') is evident.

subtriangular spicules posteriorly ('e') having a long, narrow, thickened blade.

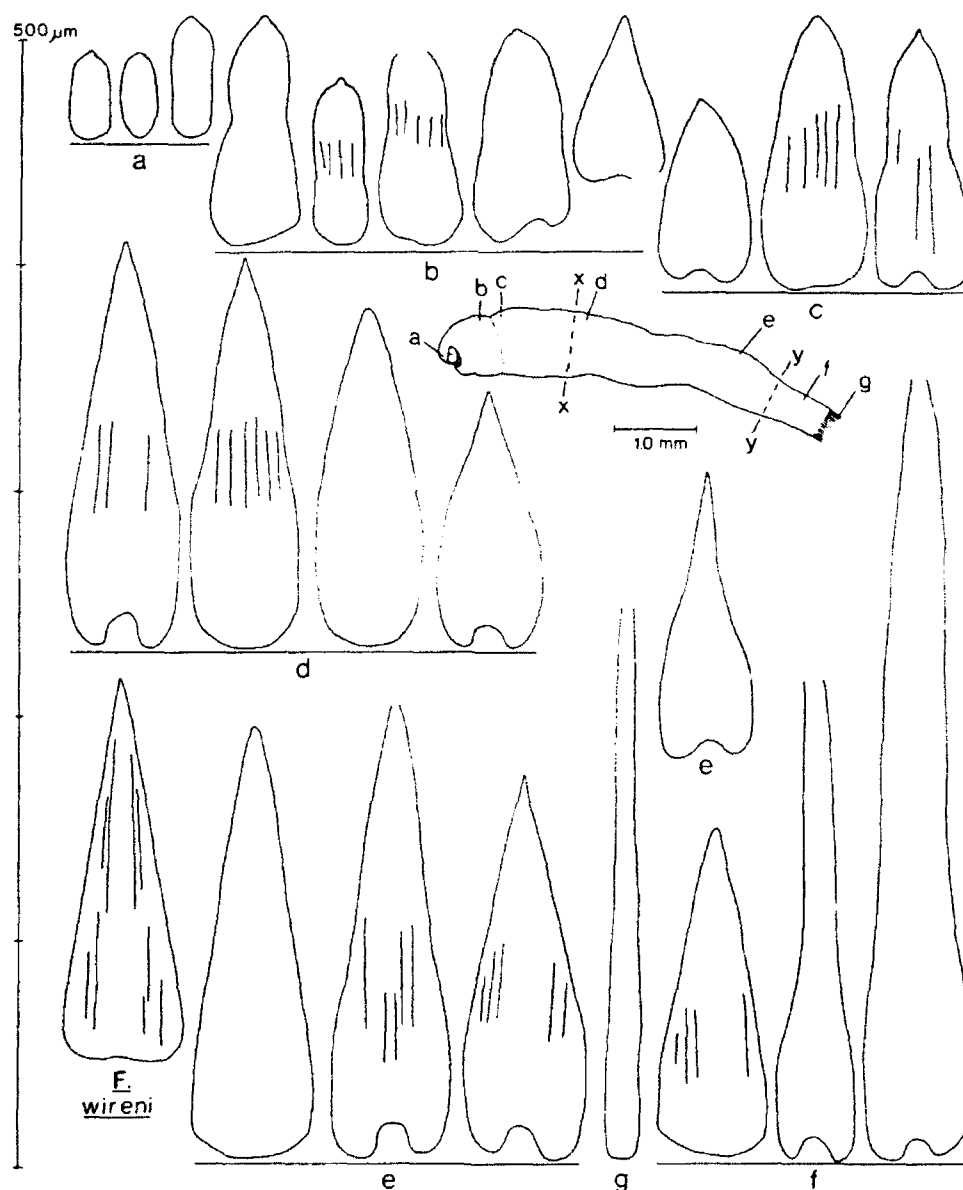
Spines surrounding cloaca are less than 300  $\mu\text{m}$  long and 8  $\mu\text{m}$  thick, shorter and thinner than longest posterior spicules; base flattened and narrow, 15  $\mu\text{m}$  in width.

**Radula.** One radula examined (Fig. 12); total length 200  $\mu\text{m}$ , nearly one third neck diameter. Cone-shaped piece 155  $\mu\text{m}$  long and anteriorly and posteriorly very narrow (15  $\mu\text{m}$ ), one quarter lateral width (60  $\mu\text{m}$ ). (See description above of *F. chistos* radula and Fig. 9 for radula morphology.) Sickie teeth 48  $\mu\text{m}$  from base to tip; tips curve towards each other nearly to touch. Tanned portion of triangular plate shaped like inverted base of

heart and bears on each side a broad, tanned apophysis extending only slightly onto sickle tooth. Connections to second pair of denticles lying alongside sickle teeth were not seen. Lateral membranes short, about 70  $\mu\text{m}$  in length, extend less than one quarter length of cone.

**Distribution.** Three specimens were taken from two stations at 120 and 130 m with mixed mud and sand in Bass Strait (Table 1).

**Closely related species.** *Falcidens lipuros* and *F. chistos* may at first be confused when they are found in the same sample, but the greater anterior trunk width and longer posterior spicules in *F. lipuros* quickly distinguish them



**Fig. 11.** Spicules of *Falcidens lipuros* n.sp. and *F. wireni* (Nierstrasz) (redrawn from Nierstrasz, 1902, fig. 205, scale unknown). 'a'-'g', spicules from paratype no. 1 figured at upper right: 'a', from oral region; 'b', from neck; 'c', from anterior trunk; 'd', 'e', from anterior and posterior part of posterior trunk; 'f', from posterior; 'g' from around cloaca. Line x-x, division between anterior and posterior trunk; y-y, division between posterior trunk and posterior. Greatest thicknesses for body regions are: 'a', 4  $\mu\text{m}$ ; 'b'-'e', 7.5-8  $\mu\text{m}$ ; 'f', 10  $\mu\text{m}$ ; 'g', 8  $\mu\text{m}$ .

under a dissecting microscope. Under a compound microscope, the spicules are distinctive.

*Falcidens wireni* is a species 11 mm long described by Nierstrasz (1902) from 1,570 m in the Banda Sea at 4°24.3'S, 129°49.3'E; from Nierstrasz's drawings (fig. 204) and description it is similar to *F. lipuros* in being wider anteriorly (more than 1 mm) than posteriorly (1 mm), in lacking a tail-like posterium, and in having a flat, blunt anterior end. The illustrated spicule of *F. wireni* (fig. 205A; redrawn here, Fig. 11) is somewhat like those of *F. lipuros* in general proportions of length to width and in having longitudinal ridges; however, the sides are straight rather than convex and the ridges are not restricted to the region of the waist. The radula drawings are inadequate for comparison.

A species of *Falcidens* similar to *F. lipuros* occurs on the slope off south-east Victoria between 363 and 800 m. cursory examination shows it to have spicules that are shorter and keeled with fine parallel ridges extending far distally on the blade.

*Falcidens macrafrondis* n.sp.

Figs 2E, 13, 14; Table 1

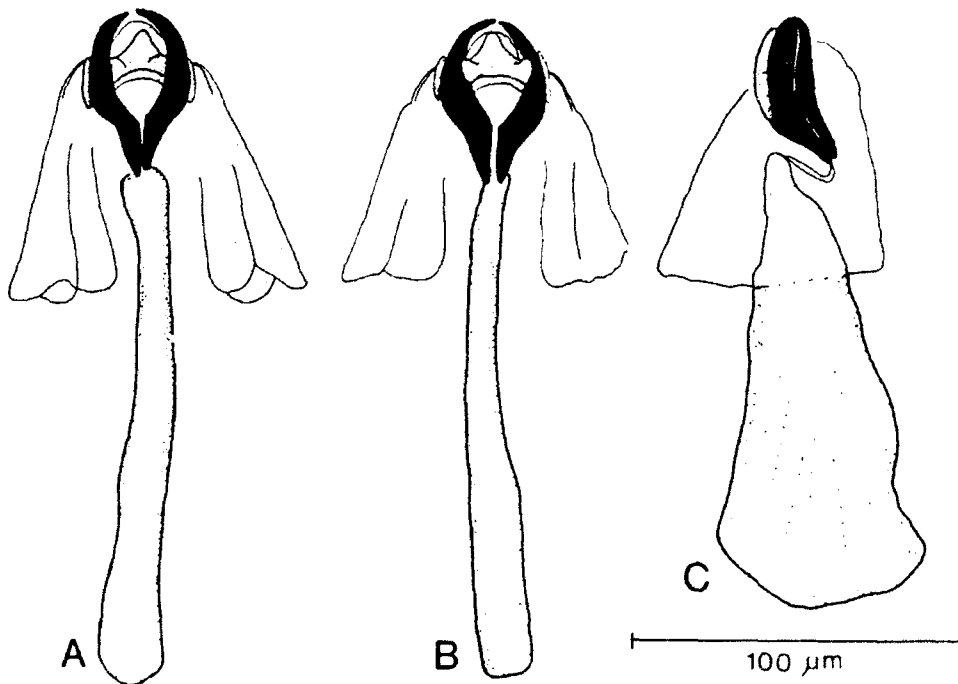
**Type material.** HOLOTYPE: off Wollongong, NSW, 34°27'26"S, 151°27'E, 1200 m. AM C156228 (wet specimen, spicule slide. Second spicule slide MV F54193). PARATYPE: type locality. AM C156229.

**Diagnosis.** Small for genus, less than 4.5 mm long by 0.5 greatest diameter, posterium probably elongate and narrow; trunk spicules triangular, very large and thick for body size, more than 300  $\mu$ m in length and 150  $\mu$ m in base width, 10  $\mu$ m or more thick, distally pointed, blade with numerous sharp longitudinal ridges and broad keel, waist not distinct; radula cone short (60  $\mu$ m) relative to tooth length (45  $\mu$ m), total length (100  $\mu$ m) about one fifth neck diameter.

**Etymology.** From *macra*, large and *frons*, leaf.

**Description.** *External morphology.* Two specimens collected have been distorted by stretching and length of body divisions cannot be determined (Fig. 13). Total stretched length about 4.5 mm; width of neck, which is not stretched, about 0.5 mm. Posterium presumably elongate, body-wall musculature weak. Probably no anterior constriction between neck and anterior trunk. Paratype female, as determined in glycerine-squashed preparation, with largest egg 32 by 45  $\mu$ m, size possibly indicates immature specimen of average adult body length (see Scheltema, 1987). Spicules remarkably large for body size, even in oral area; spicules project from neck and withdrawn mouth, but presumably flat lying on trunk, although most trunk spicules lost from specimens. Ring of long spicules surrounds relatively large, rounded cloaca (0.4 long by 0.3 mm wide); tips of spicules broken off in holotype. Shape of oral shield not known; dorsoterminal sensory organ not evident.

*Spicules.* Spicules flat and range in size from about 200 to 350  $\mu$ m in length (Fig. 14) with broad base 70 to 150  $\mu$ m



**Fig. 12.** Radula of *Falcidens lipuros* n.sp., paratype no. 1. A, B, C: posterior, anterior, and lateral views, respectively (cf. Fig. 9). Lateral view somewhat tilted and foreshortened.

wide; those that ring cloaca 30  $\mu\text{m}$  in width. Spicules from most anterior end large, especially those ventral to mouth (120  $\mu\text{m}$  long). Blades have broad keel and numerous fine, sharp, longitudinal ridges that run fan like, converging distally (Fig. 2E). Waist not distinct. Spicules are thickest at keel, 10  $\mu\text{m}$  or more; entire spicule flat and thick, 7  $\mu\text{m}$  over its greater area in spicules 200  $\mu\text{m}$  long, and 9 to 10  $\mu\text{m}$  in spicules 350  $\mu\text{m}$  long. Distal end sharply pointed; edges often becoming concave in outline near tip. Proximal end of base straight or somewhat indented.

**Radula.** Radula small, 100  $\mu\text{m}$  in total length (Fig. 13) and about one fifth neck diameter. Cone only 60  $\mu\text{m}$  long, hardly longer than sickle teeth, which are 45  $\mu\text{m}$  long; such a short cone may indicate early growth in immature specimen. Anterior cone width 15  $\mu\text{m}$ ; lateral width, 38  $\mu\text{m}$ , about 2.5

times greater. Triangular plate approaches bar shape; has 3 distinct little denticles that bend towards sickle teeth. Apophyses consist of pair of denticles. Lateral membranes short, about 35  $\mu\text{m}$ , extend down only one tenth length of cone.

**Distribution.** Only two specimens from 1200 m off Wollongong, New South Wales, are known (Table 1).

**Closely related species.** There are no known species close to *F. macrafrondis* with its large spicule size relative to body size.

### *Falcidens* spp.

A single specimen of a species with a long posterium was collected from Bass Strait at 1,120 m (Stn Q63 i, Table 1).

### Prochaetodermatidae Salvini-Plawen, 1969

**Diagnosis.** Chaetodermomorpha with large, cuticular jaws and small, distichous radula with 8-13 rows of paired teeth on unipartite radular membrane; each tooth with medial serrated membranous brush and lateral wing (Fig. 17D), radular membrane with tooth-like projections that extend along each tooth (Fig. 17B). Oral shield divided, often bordered by large spicules; posterium usually tail like; trunk not divided (Fig. 15); dorsoterminal sensory organ present but not evident (Haszprunar, 1987). Genera differentiated on basis of nonoverlapping character states of spicules shared by several species, some still undescribed (Scheltema, 1985).

### *Rhabdoderma* n.gen.

**Type species.** *Rhabdoderma australe* n.sp.

**Diagnosis.** With characters of the family. Spicules rod like, symmetrical or somewhat asymmetrical, long, thick, pointed, flattened, lacking obvious ornamentation; base longer than blade on trunk spicules (Figs 2F, 16). Spicules of trunk bound to body and arranged obliquely; they diverge on each side of ventral midline, spiral up dorsally and posteriorly, and meet at angle along dorsal midline (Fig. 15). Differentiated from *Chevroderma* Scheltema, 1985 by lack of longitudinal groove and chevron-shaped cross grooves on spicules.

**Distribution** (based largely on undescribed species). Off south-eastern Australia; north-eastern Pacific; western Atlantic from south of Cape Hatteras to the Argentine Basin; eastern Atlantic from West European Basin to Namibia Basin.

**Etymology.** From *rhabdos*, a rod.

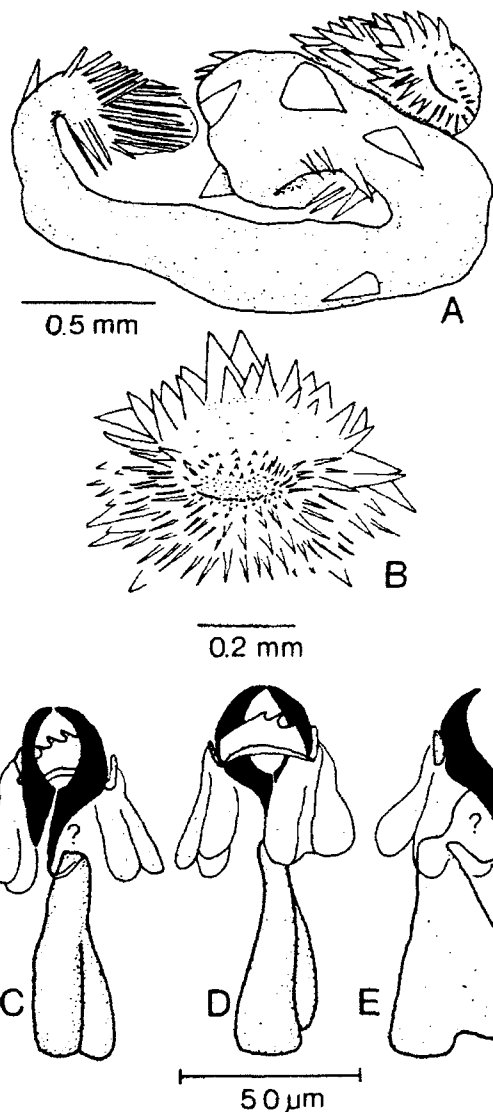


Fig. 13. *Falcidens macrafrondis* n.sp., holotype (A,B) and radula of paratype (C-E). Spicules illustrated on the trunk of the holotype (A) are the only ones remaining in this view; spicules ringing the cloaca are broken. C, D, E: posterior, anterior, and lateral views, respectively (cf. Fig. 9).

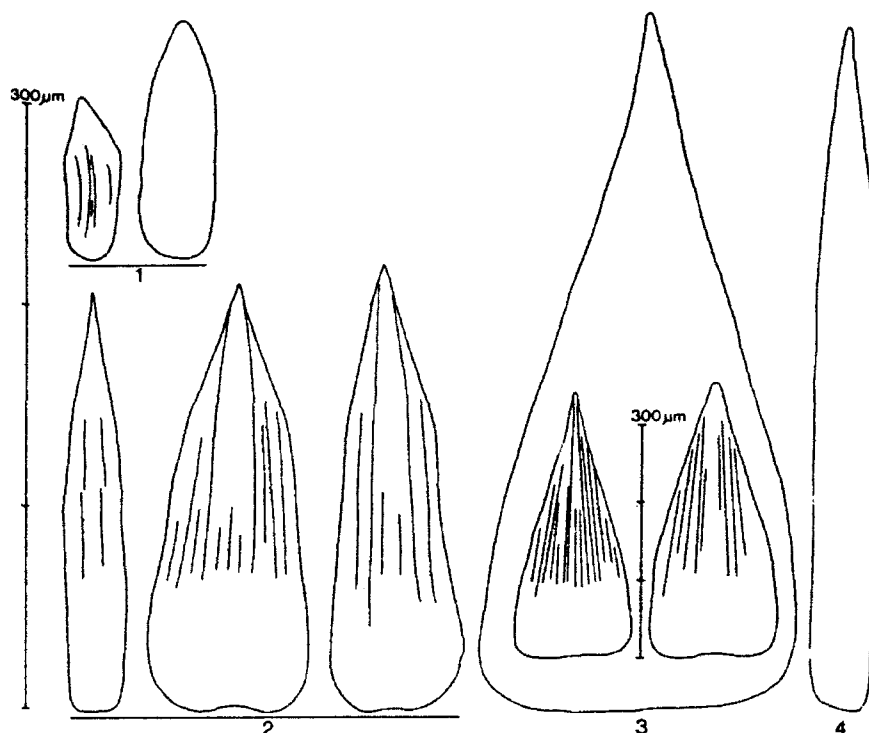


Fig. 14. Spicules of *Falcidens macrafrondis*, paratype: 1, probably from anteriormost end; 2 and 3, trunk spicules, but spicule on left perhaps from posterium; 4, one of the spicules ringing the cloaca, drawn from glycerine-squashed preparation. In 3, large spicule in outline is at the same magnification as spicules labeled 2; spicules within the outline are the same size as the outline but drawn at less magnification. Greatest thicknesses are: 1, 9  $\mu\text{m}$ ; 2, 3, greater than 10  $\mu\text{m}$ ; 4, not determined.

*Rhabdoderma australe* n.sp.

Figs 2F, 15, 16, 17; Table 1

**Type material.** HOLOTYPE: off Wollongong, NSW, 34°27'–26'S, 151°27'E, 1,200 m. AM C156230 (wet specimen, spicule slide. Second spicule slide, MV F54196). DESCRIBED PARATYPES: No. 1: type locality. AM C156231. No. 2: Bass Strait, 38°55.6'S, 148°46.4'E, 1,730 m (RV *Tangaroa*, Stn Q635, pipe dredge, 16 Nov. 1981). MV F54195.

**Diagnosis.** Large and broad prochaetodermatid, largest specimens more than 5 mm long by 1 mm in trunk diameter; posterium about one third total length; trunk translucent, spicules up to 400  $\mu\text{m}$  long, narrow (less than 50  $\mu\text{m}$ ), and thick (10  $\mu\text{m}$  or more), crossing at acute angle mid-dorsally, ornamented with fine striations, blade short relative to base, waist indistinct or lacking, base usually tapered; cloaca conical, spicules not in distinct ring; oral shield spicules not obviously larger than surrounding spicules; teeth of radula and jaws large, 175 and 825  $\mu\text{m}$  long, respectively, central plate D-shaped, 45 x 18  $\mu\text{m}$ .

**Description.** *External morphology.* *Rhabdoderma australe* is large for a prochaetodermatid both in length (up to 5.2 mm) and in trunk diameter (up to 1.1 mm) (Fig. 15). Posterium one third to two fifths body length and about one half body width. Trunk translucent; spicules closely bound to body and meet at a pronounced angle mid-dorsally.

Spicules of anterior end large and stand out somewhat from body; on opaque posterium spicules extend away from body. Oral shield spicules not obviously larger than surrounding spicules; oral shield does not cover entire oral area of anterium in some specimens. Cloaca conical and not surrounded by discrete ring of spicules; spicules of cloaca brush like.

**Holotype:** total length 4.8 mm; trunk 2.9 by 1.1 mm; posterium 1.9 by 0.5 mm; index of posterium length to trunk length 0.66. Oral shield (left half of pair) 0.13 by 0.20 mm, index 2.36.

**Spicules.** Spicules long, thick, curved slightly toward body (Fig. 16); numerous faint striations run lengthwise (Fig. 2F). Base longer than blade except in a few spicules from anterior end ('a') and in those from posterium ('d'). Sides of base gently convex; in some spicules convexity greater on one side than the other and spicules slightly asymmetrical (cf. genus *Chevroderma* Scheltema, 1985). Proximal end of base rounded and either tapered or untapered, or straight and either untapered or flared. Short blade has rounded point distally; side edges either continue curve of base or set off by slight indentation at waist. Spicules thickest medially; isochromes symmetrical.

At anterior end (region 'a') spicules long (up to 160  $\mu\text{m}$ ), thick (7–10  $\mu\text{m}$ ), and up to 40  $\mu\text{m}$  wide; distal ends of blade bluntly rounded and waist usually distinct.

Most spicules from lateral and dorsal trunk (regions 'b<sub>1</sub>' and 'c<sub>1</sub>') are 300 to nearly 400  $\mu\text{m}$  long, 35–45  $\mu\text{m}$  wide, and 9 to more than 10  $\mu\text{m}$  thick, but spicules from ventral

body surface ('b<sub>2</sub>' and 'c<sub>2</sub>') are smaller, less than 200 µm long, 25-30 µm wide, and 5 to 8 µm thick, with usually sharper distal points. Scattered amongst most usual spicules are other types: (1) short (length 160 µm), thin (7 µm), blade narrow and sharply pointed with distinct waist; (2) long (up to 350 µm), thick (greater than 10 µm), with edges of sides parallel and 9-µm isochromes running parallel to each other to straight proximal end of base, waist not distinct; (3) similar to type (2) except shorter (80-160 µm long) and with flared base; (4) short (225 µm in length) and broad (45 µm width) with a broad blade. Some specimens have many type 2 spicules, and some have few.

Spicules of posterium (region 'd') long and narrow, from 350 µm up to 425 µm long and 30 µm or less in width. Blades longer and thicker (up to 10 µm) than base which is scarcely or not at all tapered.

Spicules from cloaca (region 'e') narrow, curved rods 10 µm thick and somewhat more pointed distally than proximally; same length (up to 425 µm) as those from posterium.

**Radula.** Radula and jaws in *F. australe* large; teeth in 12-13 rows, first 3 pairs worn. In a specimen with trunk measuring 3.0 by 1.1 mm (paratype no. 1), teeth 175 µm long with broad lateral wing (Fig. 17). Jaws 825 µm long by 390 µm wide. Membranous lateral tooth-like extensions of radular membrane large and obvious, reaching half way up sides of teeth with small basal projection. Central plates

D-shaped, thin and indistinct, of average length (45-50 µm) for family, but wide, up to 18 µm. In much smaller specimen (trunk 1.6 by 0.6 mm), teeth 130 µm long, jaws 560 by 280 µm, central plates 40 by 18 µm.

**Distribution.** A total of 69 specimens were taken from the slope between 1,120 and 2,510 m off Wollongong, New South Wales, and Point Hicks, Victoria (Table 1).

### *Prochaetoderma* Thiele, 1902

**Type species.** *Chaetoderma raduliferum* Kowalevsky, 1901 by monotypy.

**Diagnosis.** With characters of the family. Spicules flat; base shorter than blade, blade triangular with median keel and sharp distal point; waist present (Fig. 1B).

**Distribution.** Eastern and western Atlantic Ocean; Mediterranean; off south-eastern Australia.

### *Prochaetoderma* sp.

Fig. 1B

A single small specimen 1.9 mm long with a very short posterium (0.19 x trunk length) was taken from 1,120 m in

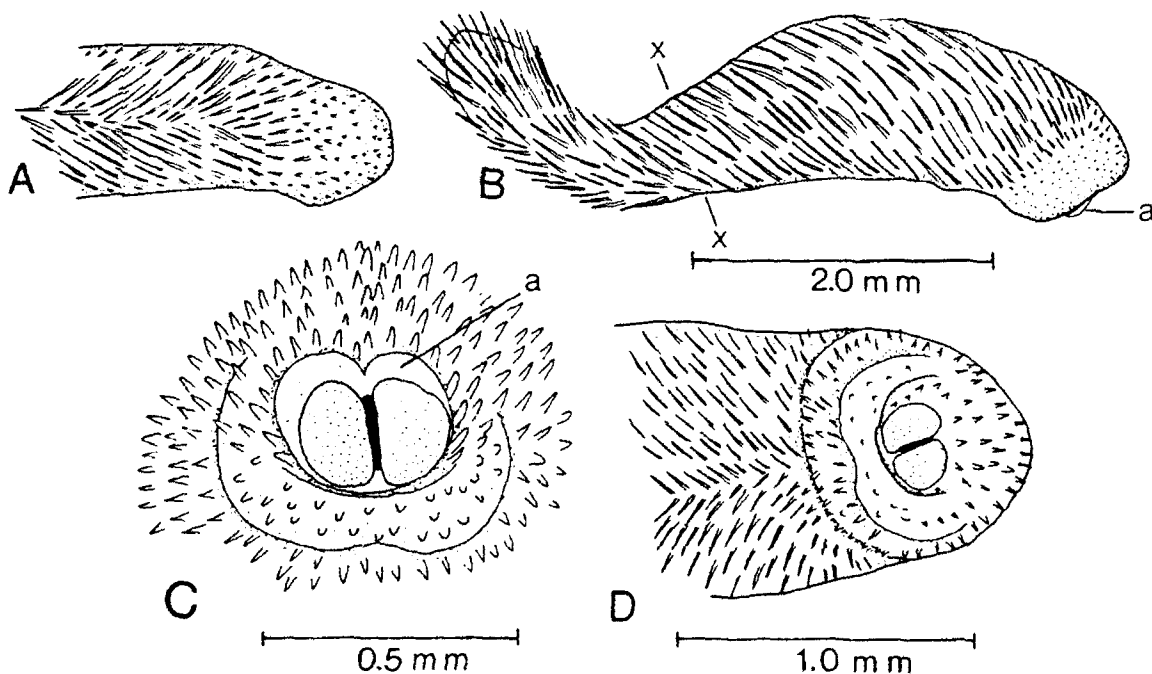


Fig. 15. *Rhabdoderma australe* n.sp., holotype. A: anterodorsal view; B: lateral view; C: anterior view, oral shield and anterior; D: anteroventral view. a, anterior; x-x, division between trunk and posterium. A and B at same scale.



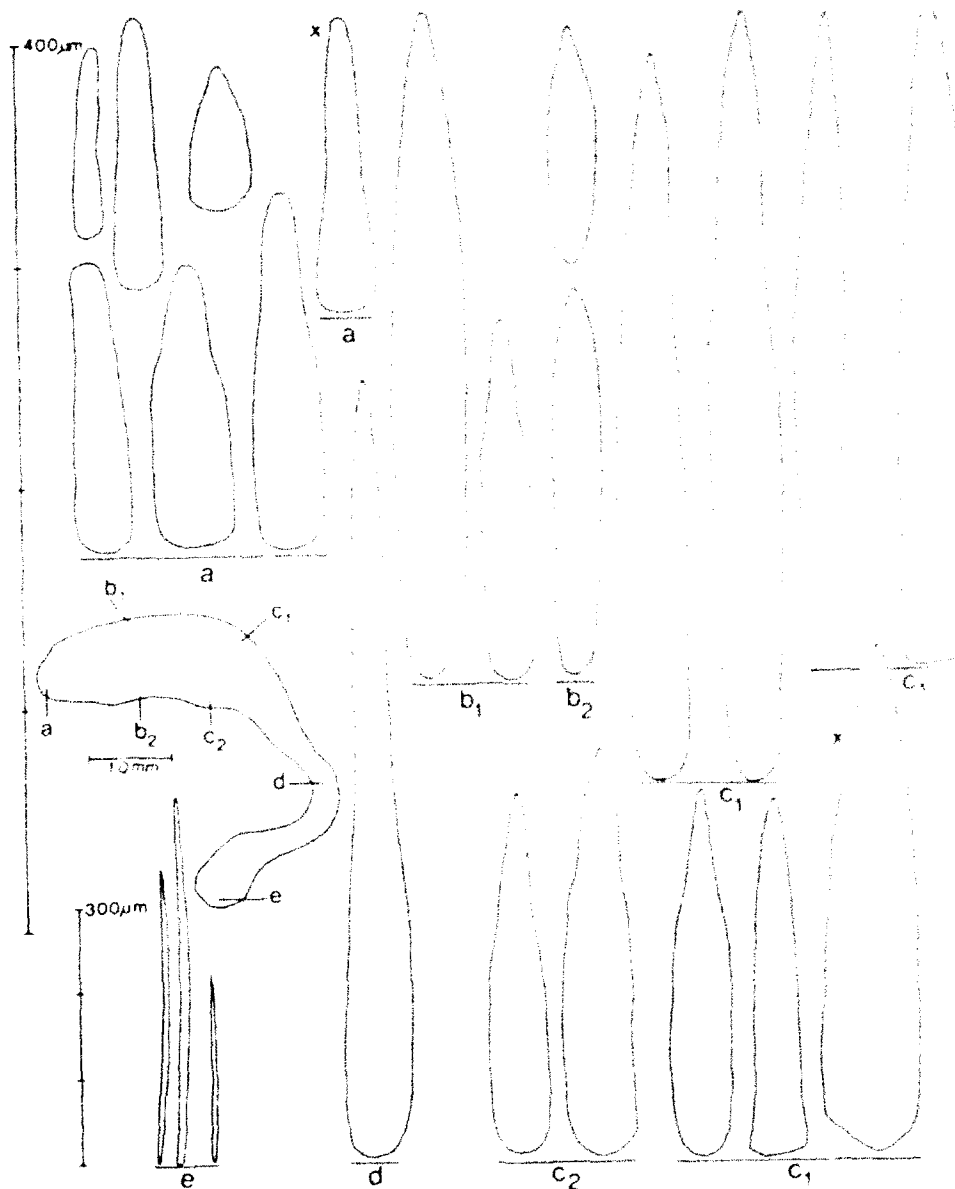
the same sample as a specimen of *R. australe* (Stn Q631, Table 1). The spicules are long for the size of the specimen, up to 300  $\mu\text{m}$ , a condition often seen in juveniles, whose spicules usually appear to be too large for them. However, eggs measured through the integument are nearly 100  $\mu\text{m}$  long, a size which indicates adult body length but not full maturity (see Scheltema, 1987).

The genus has not been recorded before from the Pacific. (*Prochaetoderma californicum* Schwabl belongs to the genus *Spathoderma*; determination based on re-examination of syntypes, not yet published.) A full

description and species designation awaits additional specimens. [New material from Slope Stn 27 provides 4 specimens (Table 1).]

#### Undetermined Prochaetodermatidae

A single specimen of a prochaetodermatid species lacking spicules was taken from 55 m in Bass Strait at R/V *Hai-kung* Stn 139 (Table 1). It is not the same as either of the above species.



**Fig. 16.** Spicules of *Rhabdoderma australe* n.sp. Spicules are from body regions 'a'-'e' of paratype no. 1 as indicated in figure, except for two marked x, which are from other specimens. Thickest spicules from each body region are 10  $\mu\text{m}$  or more thick, except for ventral spicules  $b_1$  and  $c_1$ , which are up to 7 and 8  $\mu\text{m}$  thick, respectively. Ornamentation of fine lengthwise striations (see Fig. 2F) is not shown. The posterium of paratype no. 1 is unnaturally stretched.

### Undetermined Chaetodermomorpha

A single specimen of a small (2.5 mm), transparent chaetodermatid with thin spicules thinly dispersed and deeply imbedded in the cuticle was taken from 56 m at Stn T-163 S-M (Table 1).

### Undetermined slope species

Besides the species listed in Table 1, the following new

slope species have been recently received and await description: three species of *Falcidens*, two species of *Chaetoderma*, one species of *Scutopus*, and one species of *Limifossor*. The recorded ranges of *Scutopus* and *Limifossor* are thus extended to the western Pacific.

### Discussion

The aplacophoran fauna of the Pacific is not well known

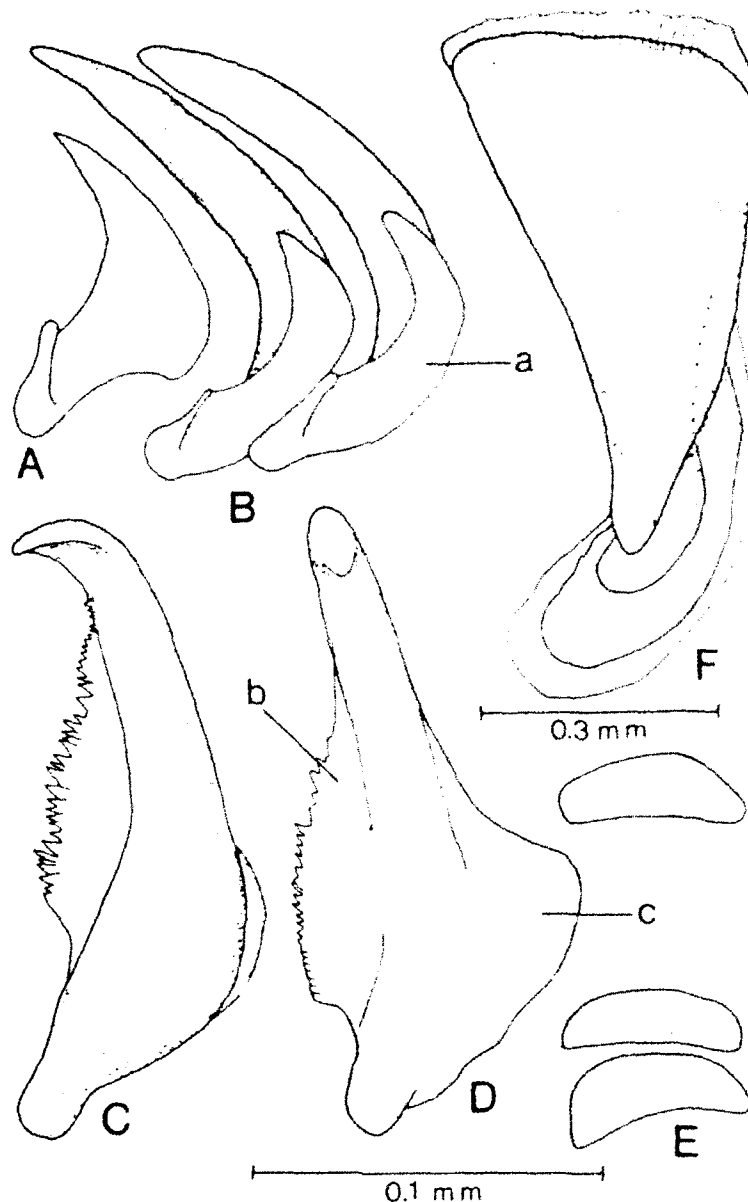


Fig.17. Radula and jaw of *Rhabdoderma australe* n.sp., paratype no. 1. A: lateral tooth-like extension of radular membrane; B: third and fourth teeth from proximal end of radular sac, lateral view, anterior to right, lateral tooth-like extensions ('a') in natural position; C, D: two views of individual teeth showing medial denticulate membrane, or brush ('b'), and lateral wing ('c') (bent over in view C); E: central plates; F: left jaw, lateral view from inside; mouth opens at right.

Most of the species of Pacific Chaetodermomorpha that have previously been described were collected by four surveys: the *Siboga* Expedition (Nierstrasz, 1902; Stork, 1941), the U.S. Fish Commission vessel *Albatross* (Heath, 1911), the Pacific Expedition of the Allan Hancock Foundation, University of Southern California (Schwabl, 1963), and the USSR Academy of Sciences in the Sea of Japan (Ivanov, 1984). The great *Challenger* Expedition collected only one aplacophoran in the Pacific (Selenka, 1885). Several additional descriptions not part of surveys or expedition reports have also been published (Okuda, 1943; Salvini-Plawen, 1972; Osorio & Tarifeño, 1976; Scheltema, 1985). The total number of Chaetodermomorpha species so far described is small, about 36 (Table 2). Some of this number are suspected to be synonyms; species names known to be synonyms from examination of new material and re-examination of types are reflected in the table numbers.

The 16 new species collected off south-east Australia increase the number of Pacific Chaetodermomorpha by a half. The vertical distributions of these species by genus are similar to those of previously described species, with the exception of the genus *Chaetoderma* (Table 2). *Chaetoderma* is not represented at all in the south-east

Australian shelf collections, and only by one species on the upper slope, whereas in the rest of the Pacific, species of *Chaetoderma* occur mostly at depths less than 1,000 m. Furthermore, in the family Chaetodermatidae, the genus *Falcidens* off south-east Australia, unlike the rest of the Pacific, has more species than the genus *Chaetoderma*. This preponderance of *Falcidens* species perhaps reflects speciation in that region.

Two species of Chaetodermomorpha off south-east Australia are common. *Falcidens chiastos* occurs at densities up to 180 m<sup>2</sup> in 20 of the 46 shelf samples that contain Aplacophora. The slope prochaetodermatid species *Rhabdoderma australe* also appears to be abundant at depths below 1,000 m, although quantitative data are lacking (Table 1). Some members of the Prochaetodermatidae are known to be among the most numerically abundant animals in the deep-sea fauna, including a Pacific species in the closely related genus *Chevroderma* (Scheltema, 1985).

The genus *Psilodens* Salvini-Plawen, 1977 (= *Scutopus partem*) does not occur in the shelf or slope samples, although it is in collections from both the east Pacific and Indian Ocean (the latter is unpublished). An uncommon but widespread genus, it probably will eventually be found

Table 2. Distribution of Chaetodermomorpha in the Pacific by depth.

Genus	Depth m <sup>1</sup>	Previously Described <sup>2</sup> No. Species	New spp. off South-east Australia No. Species	Total Species
<i>Scutopus</i>	<200	0	0	0
	200-1,000	1	1	2
	>1,000	0	0	0
<i>Psilodens</i>	<200	0	0	0
	200-1,000	0	0	0
	>1,000	1	0	1
<i>Limifossor</i>	<200	0	0	0
	200-1,000	2	1	3
	>1,000	0	0	0
<i>Falcidens</i>	<200	1	2	3
	200-1,000	1	3	4
	>1,000	3	2	5
<i>Chaetoderma</i>	<200	4	0	4
	200-1,000	18	1	19
	>1,000	3	2	5
Prochaeto- dermatidae (genera combined)	<200	0	1	1
	200-1,000	1	0	1
	>1,000	1	2	3
TOTAL		36	15 <sup>3</sup>	51

<sup>1</sup> <200 m - shelf species, 200-1,000 m - upper slope species, including those that also extend onto the shelf, >1,000 m - lower slope or abyssal species, including those that also extend onto the upper slope or, in a few cases, also onto the shelf. <sup>2</sup> Numbers reflect known, but unpublished, synonyms. Data from Heath (1911), Ivanov (1984), Nierstrasz (1902), Okuda (1943), Osorio & Tarifeño (1976), Salvini-Plawen (1972), Scheltema (1985), Schwabl (1963), Selenka (1885), and Stork (1941). <sup>3</sup> A single specimen of a shelf species of undetermined affinity is not included (Sm 163 S-M, Table 1).

off the Australian coast.

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### References

- Haszprunar, G., 1987. The fine morphology of the osphradial organs of the Mollusca. IV. Caudofoveata and Solenogastres. Philosophical Transactions of the Royal Society of London (B) 315: 37-73.
- Heath, H., 1911. The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific...by the "Albatross"...Memoirs of the Museum of Comparative Zoology 45(1): 1-179.
- Heppell, D., 1963. *Chaetoderma* Lovén, 1844 (Mollusca), and *Chaetodermis* Swainson, 1839 (Pisces): proposed addition to the official list of generic names. Z. N. (S.) 1250. Bulletin of Zoological Nomenclature 20(6): 429-431.
- International Commission on Zoological Nomenclature, 1966. Opinion 764, *Chaetoderma* Lovén, 1844 (Mollusca), and *Chaetodermis* Swainson, 1839 (Pisces): added to the official list of generic names.
- Ivanov, D.I., 1981. [*Caudofoveatus tetradens* gen. et sp. n. and diagnosis of taxa in the subclass Caudofoveata (Mollusca, Aplacophora)]. Zoologicheskii Zhurnal 60: 18-28 [In Russian].
- Ivanov, D.I., 1984. [Caudofoveata (Mollusca, Caudofoveata) in Peter the Great Bay. pp. 28-41. In 'Hydrobiological Research of Bays and Inlets of Primorye' (A.I. Kafanov, ed.). Far East Center, USSR Academy of Sciences, Vladivostok. [In Russian].]
- Nierstrasz, H. F., 1902. The solenogastres of the Siboga-Expedition. Siboga-Expeditie 47. E. J. Brill, Leyden. 46 pp.
- Okuda, S., 1943. The fauna of Akkeshi Bay. XIV. Solenogastres. Annotationes Zoologicae Japonenses 22: 11-14.
- Osono, C. & E. Tarifeño, 1976. A new species of Aplacophorous mollusk from the southeastern Pacific Ocean: *Chaetoderma araucanae* spec. nov. (Mollusca: Caudofoveata: Chaetodermatidae). Veliger 19: 94-89.
- Salvini-Plawen, L. von, 1972. Die Caudofoveata des Mittelmeeres und das Genus *Scutopus* (Mollusca, Aculifera). pp. 27-51. In 'Fifth European Marine Biology Symposium' (B. Battaglia, ed.). Piccin Editore, Padua.
- Salvini-Plawen, L. von, 1977. Caudofoveata (Mollusca) des Forschungsprojektes Polyméde. Bulletin du Muséum national d'Histoire naturelle, 3<sup>e</sup> sér., 447: 413-421.
- Salvini-Plawen, L. von, 1984. [Comments on *Chaetoderma* and *Crystallophrisson* (Mollusca, Caudofoveata)]. Zoologicheskii Zhurnal 63: 171-175. [In Russian.]
- Scheltema, A.H., 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). Zeitschrift für Morphologie der Tiere 72: 361-370.
- Scheltema, A.H., 1976. Two new species of *Chaetoderma* from off west Africa (Aplacophora, Chaetodermatidae). Journal of Molluscan Studies 42: 223-234.
- Scheltema, A.H., 1981. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. Malacologia 20: 361-383.
- Scheltema, A.H., 1985. The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca: Chaetodermomorpha). Biological Bulletin (Woods Hole) 169: 484-529.
- Scheltema, A.H., 1987. Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yonsei*. Marine Ecology Progress Series 37: 171-180.
- Scheltema, A.H., 1988. Ancestors and descendants: relationships of the Aplacophora and Polyplacophora. American Malacological Bulletin 6: 57-68.
- Schwabl, M., 1963. Solenogaster mollusks from southern California. Pacific Science 17(3): 261-281.
- Selenka, E., 1885. Report on the Gephyrea collected by H.M.S. *Challenger* during the years 1873-1876. Report on the Scientific Results...of H.M.S. *Challenger* 13(2): 25 pp.
- Stork, H.A., 1941. Solenogastren der Siboga-Expedition. Siboga-Expeditie 47b: 45-70. E.J. Brill, Leyden.

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# ANCESTORS AND DESCENDENTS: RELATIONSHIPS OF THE APLACOPHORA AND POLYPLACOPHORA

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## ABSTRACT

Four organ systems, pericardium of primitive mollusks, shell ontogeny and spicule formation in chitons and aplacophorans, chaetoderm oral shield, and aplacophoran radula, are described and their relationships discussed. The discussion suggests: (1) a coelomate ancestor of the mollusks; (2) a polyphyletic origin of shell, one for Conchifera and another for chitons; (3) a single class Aplacophora containing two taxa, the Chaetodermomorpha and Neomeniomorpha; (4) an archimolluscan radula with a pair of separate radular membranes bearing rows of single teeth. Evidence is presented that contradicts the following hypotheses: (1) an acoelomate origin of mollusks; (2) the division of aplacophorans into two classes; (3) the derivation of the univalved molluscan shell from a common stem with the eight-shelled chitons. The concept of a subphylum Aculifera is rejected as unnecessary since it holds no essential information.

Hypotheses of early molluscan evolution in the last fifteen years have proposed an acoelomate, turbellariomorph pre-molluscan ancestor with a mucoid dorsal cover and a broad, ciliated locomotory sole through which opened a mouth (Fig. 1) (Salvini-Plawen, 1972, 1980, 1985; Haas, 1981; Boss, 1982; Poulicek and Kreusch, 1983; see also Fretter and Graham, 1962; Stasek, 1972). According to such theories, this pre-mollusk gave rise to an archimollusk with a spiculate integument, an unpaired radular membrane, and a mouth that opened through the ventral locomotory surface. The archimollusk then gave rise to two major taxa, the burrowing aplacophorans (Chaetodermomorpha = Caudofoveata) and an "adenopod", with seven transverse rows of scales and a head separated from the sole. The second group of aplacophorans, the footed Neomeniomorpha (= *Solenogastres sensu* Salvini-Plawen), have split off from the hypothetical "adenopod", the latter giving rise to an "archiplacophoran" with plates formed from coalesced scales. The "archiplacophoran" in turn was the precursor of the Polyplacophora on one hand and the rest of the shelled mollusks, the Conchifera, on the other (for recent accounts and bibliographic references, see Runnegar and Pojeta, 1985; Wingstrand, 1985; Salvini-Plawen, 1985). The subphylum Aculifera, recognized by Haas (1981) and formerly, but no longer, by Salvini-Plawen (cf. 1972, 1980), includes the extant Aplacophora and Polyplacophora as well as the hypothetical archimollusk, adenopod and archiplacophora; all other mollusks form the subphylum Conchifera. Salvini-Plawen (1980) considers the Chaetoder-

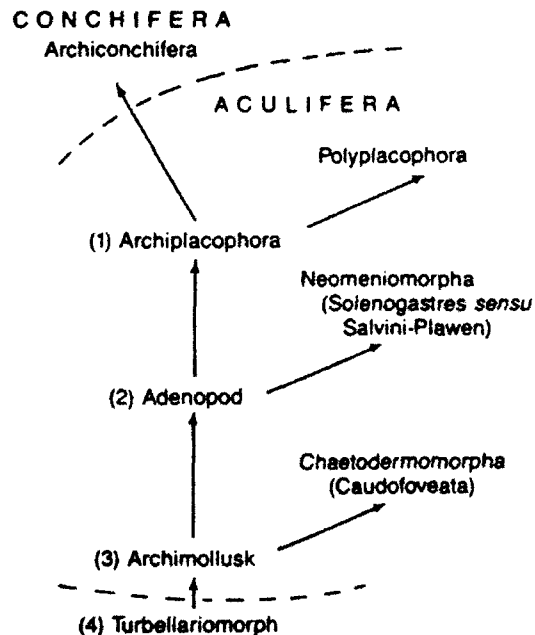


Fig. 1. Phylogeny of the Mollusca (adapted in part from Salvini-Plawen, 1980; Haas, 1981; Poulicek and Kreusch, 1983). Questioned in the text is the validity of: (1) an archiplacophoran origin of the Conchifera; (2) separation of the aplacophoran taxa Chaetodermomorpha and Neomeniomorpha by the existence of an Adenopod; (3) an archimolluscan radula with an undivided radular membrane; (4) an acoelomate ancestor. Compare with figure 14.

momorpha to belong to the subphylum Scutopoda; all remaining mollusks, including the Neomeniomorpha, constitute the subphylum Adenopoda.

Evidence presented here draws on recent observations or experiments on shell and radula formation, the structure of the oral shield of the burrowing aplacophorans, and the size of pericardial spaces in three primitive molluscan classes. The evidence raises questions about the validity of four hypotheses: (1) there is a monophyletic (archiplacophoran) origin of chitons and conchiiferan mollusks; (2) the two aplacophoran taxa belong to two separate classes; (3) the most primitive molluscan radula had an undivided radular membrane; (4) the ancestor of mollusks was acoelomate (Fig. 1).

## SHELL AND SPICULES

### APLACOPHORA AND POLYPLACOPHORA

The Aplacophora and Polyplacophora have been classified together either as the Amphineura because of their similar ladder-like nervous systems (not examined here), or as the Aculifera because of their similar integumental structures: papillae, spines, and cuticle. Indeed, these anatomical relationships between the two groups have been used to justify the inclusion of Aplacophora within the Mollusca (for historical reviews, see Hyman, 1967; Scheltema, 1978),

although they are better regarded as symplesiomorphic traits, shared primitive states that do not necessarily show close evolutionary relationships.

Beedham and Trueman (1968) found similarities in the histochemistry of aplacophoran and chiton integumental cuticle and concluded that "the cuticle of the Aplacophora is tentatively equated with an early mucoid stage in the evolution of the molluscan shell... [The cuticle of *Acanthochiton*] has in addition a discrete inner cuticular layer which may act as a semi-conducting membrane in the deposition of calcareous plates" (p. 443). The papillae of Aplacophora and Polyplacophora are probably homologous (F. P. Fischer, pers. comm.); the papillae and aesthetes of Polyplacophora are likewise homologous (Fischer et al., 1980; Fischer, 1988).

The process of calcareous spicule formation, most recently investigated by Haas (1981), is alike in aplacophorans and chitons (Fig. 2). In both taxa, a spine is secreted extracellularly within an invagination of a single cell. A basal cell secretes calcium carbonate, and as the spicule grows beyond this cell, a crystallization chamber is sealed off by a collar of neighboring cells. The megaspines in chitons, which do not occur in Aplacophora, are formed by a proliferation of the original single basal cell.

The attempt to find further similarities in calcium carbonate deposition that would link the Aplacophora and Polyplacophora by examining embryogenesis has led to less conclusive comparisons. Larval development in the two

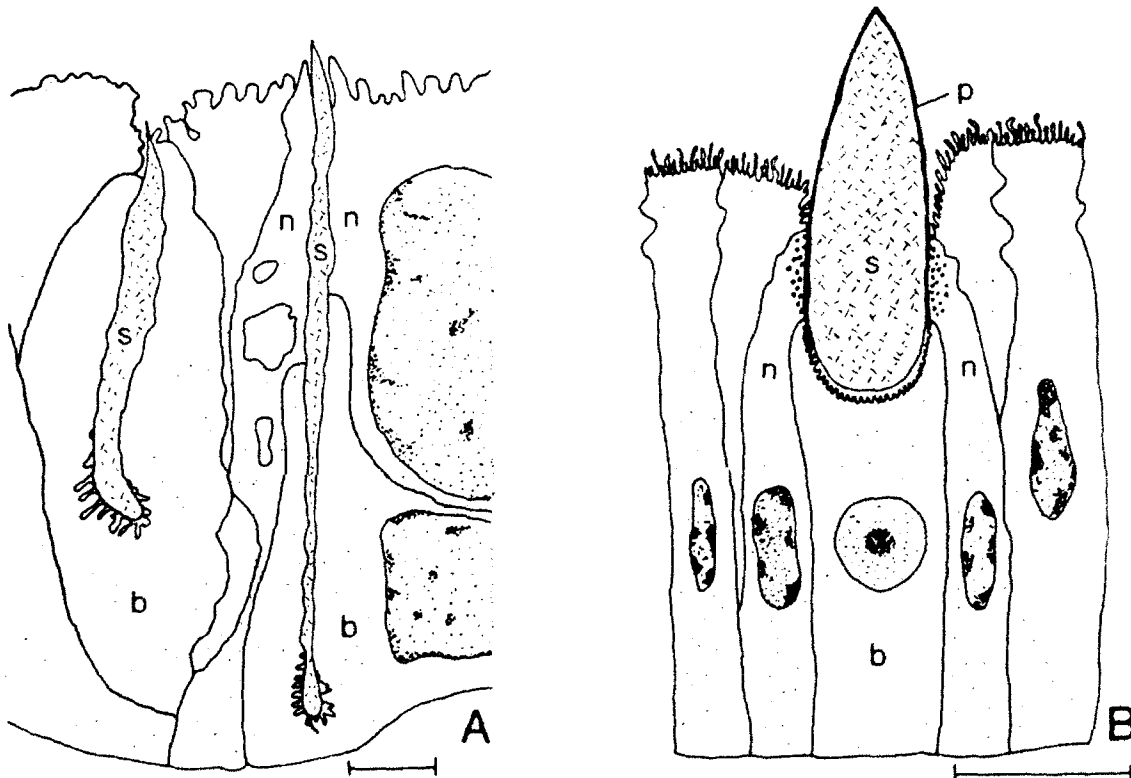


Fig. 2. Spicule formation in Aplacophora and Polyplacophora. A. Primitive Neomeniomorpha. B. *Lepidochitona cinerea* (Linnaeus). An organic pellicle has not been demonstrated around spicules of the Aplacophora. (After Haas, 1981.) (b, basal cell; n, neighboring cell; p, organic pellicle; s, spicule). Scale bars = 1  $\mu$ m.

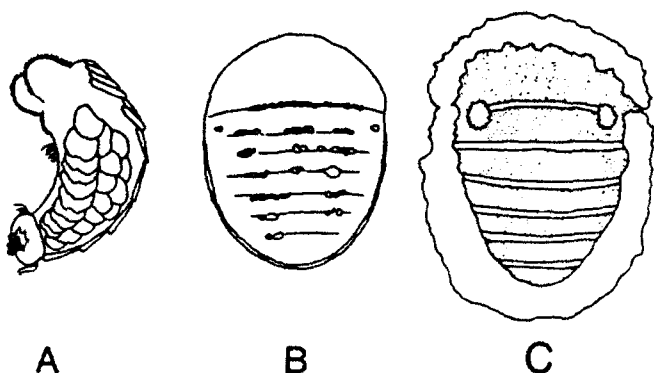


Fig. 3. Reported ontogeny in an aplacophoran, *Nematomenia banyulensis* Puvot, and a chiton, *Lepidochitona corrugata* Reeve [= *Middendorffia caprearum* (Scacchi)]. A. Puvot's larva, a single observation, lateral view, of a metamorphosing larva of *Nematomenia* with seven dorsal calcareous "plaques", slightly imbricated and formed of rectangular, plainly juxtaposed spicules" (translated from Puvot, 1890). The larva did not survive to a juvenile stage. B. Defective shell formation in *Lepidochitona corrugata* (= *Chiton polii* (Philippi)) as illustrated by Kowalevsky (1883) with separate granules of calcium carbonate deposited along seven plate fields. Coalescence of these granules does not lead to normal growth of shell plates (see Kniprath, 1980). C. Birefringence under cross-polarized light in a normally developing *Lepidochitona corrugata* larva. Noncalcareous areas are stippled; the birefringent spicular girdle and six straight, uninterrupted anlagen of the shell plates are without stippling, as are the birefringent rosette-shaped larval eyes. (A and B after Salvini-Plawen, 1972: Fig. 29, after comparison with the original drawings of Puvot, 1890, and Kowalevsky, 1883; C drawn after photograph by Kniprath, 1980: Fig. 1b.). Scales not known.

groups is dissimilar, but Salvini-Plawen [1972, 1980, 1985 (with qualifications)] argues for homology between seven rows of spicules seen once in a single aplacophoran larva [*Nematomenia banyulensis* Puvot, Puvot (1890)] and the development of shell in the larva of the chiton *Lepidochitona corrugata* (Reeve) (= *Chiton polii* Philippi) by a coalescence of granules (Fig. 3A, B) (Kowalevsky, 1883). The rows of spicules observed by Puvot have not subsequently been seen in any other aplacophoran larvae [*Epimenia verrucosa* (Nierstrasz), *Halomenia gravis* Heath, *Neomenia carinata* Tullberg; see Hadfield (1979) for a summary]. Puvot's drawing is a lateral view, and the often-copied dorsal view showing seven rows of spicules is a hypothetical reconstruction (Salvini-Plawen, 1972; Wingstrand, 1985).

Recently, Kniprath (1980) reported from rearing experiments that in the larvae of both *Lepidochitona corrugata* [= *Middendorffia caprearum* (Scacchi)] and *Ischnochiton rissoi* (Payraudeau) the anlagen of the plates are secreted as uninterrupted rods along narrow transverse depressions, the shell or plate fields, after the development of girdle spicules (Fig. 3C). When *Lepidochitona* larvae were reared at temperatures of 14°-16°C, shell development was normal, but all larvae raised at higher temperatures of 18°-21°C were abnormal and developed granules similar to those reported by Kowalevsky (1883). These granules, even when they coa-

lesced, produced defective shell plates.

The seven "plaques" of Puvot's larval aplacophoran specimen are said to reflect the number of plates in the early fossil chiton *Septemchiton* (Hyman, 1967; Salvini-Plawen, 1980) and the seven "larval" plaques of chitons (Salvini-Plawen, 1985). However, Rolfe (1981) has shown that the most anterior plate of *Septemchiton*, a burrowing form, although greatly reduced is indeed present and that *Septemchiton* therefore has a full complement of eight plates. Although the caudal plate in chitons is usually added last during development, sometimes only after an extended period of five weeks (Pearse, 1979), it is not clear whether this time lapse reflects an ancestral chiton with only seven plates or is simply a result of development as a chiton elongates. In many adult aplacophorans with single overlapping layers of flat, leaf-like spicules, the bases of the spicules are aligned in rows that are transverse to the long axis of the animal (unpub. data); it would therefore not be surprising to find spicules lined-up in metamorphosing larvae that could be mistaken for "plaques".

Evidence for the coalescence of spines is said to be shown by three sets of broad spicules, or shields, on the head of the juvenile aplacophoran *Nematomenia protecta* (Thiele, 1913). This conclusion is based on spicule shape only, without reference to the underlying epithelium; the number of cells involved in secreting a "shield", a single cell or more than one cell, is not known, despite the inferred epithelial connection constructed by Salvini-Plawen (1985: Fig. 36D). The evidence for coalescence therefore remains unsubstantiated.

Both aplacophorans and chitons retain in common a phylogenetically early mode of calcium carbonate deposition in the form of spicules, but until further observations on aplacophoran embryogenesis prove to the contrary, close evolutionary relationship between the formation of aplacophoran spicules and chiton shells is considered undemonstrated. There is no evidence within chitons themselves that spicules have coalesced to form shell plates.

## POLYPLACOPHORA AND THE OTHER SHELLED MOLLUSKS (CONCHIFERA)

The process of shell formation in chitons is argued here to be unique among mollusks. In those gastropods, bivalves, and cephalopods for which the entire shell ontogeny has been studied, earliest calcium carbonate deposition is preceded, first, by formation of a shell-field and shell-field invagination from part of the dorsal ectoderm and, second, by the secretion of an organic pellicle, usually equated with periostracum, over the invagination (Fig. 4A) (Kniprath, 1981; Eyster and Morse, 1984). [In the Cephalopoda, yolk interferes with invagination and, instead, ectoderm builds up in an elevated ring (Kniprath, 1981)]. Calcium carbonate is then secreted beneath the organic pellicle. In the nudibranch *Aeolidia papillosa* (Linnaeus), the early organic pellicle is overlain by long cytoplasmic processes that presumably seal off the crystallization chamber under the pellicle (Fig. 4B) (Eyster and Morse, 1984).

In chitons, no shell field invagination forms (Fig. 4C).

Deposition of a shell plate anlage takes place within a transverse depression bounded and sealed off by long, overlapping microvilli that lie beneath a gelatinous mucoid substance, certainly not periostracum, and questionably equated with a cuticle (Fig. 4C, D) (Kniprath, 1980; Haas *et al.*, 1980; Haas, 1981).

Not only are the ontogenetic processes of shell formation different in chitons and the Conchifera, but structures of the fully formed shells are also unlike and homologies are difficult to discover. Periostracum in the Conchifera, a structure conservative in manner of its secretion and in composi-

tion (Grégoire, 1972), does not exist in chitons, although Haas (1981) has demonstrated the presence of a thin cuticle, or properiostracum, overlying the tegmentum and a properiostracal groove surrounding each shell plate. There is no nacreous layer in chiton shells as found in other mollusks, and the cross-lamellar structure of the shell plates is crystallographically unique, with bundles of crystal fibers in the lamellae ordered so that their c-axis "coincides with the bisectrix of these crossing fibers" (Haas, 1981: 403) and the "whole complex acts crystallographically as a single crystal" (Haas, 1977: 392). In other molluscan cross-lamellar structures, the angle between crystal fibers is about  $110^\circ$ ; in gastropods they lie between  $90^\circ$ - $130^\circ$  (Wilbur and Saleuddin, 1983). Haas (1981) considered the cross-lamellar structure of chitons to be homologous with the nacreous layer of other shelled mollusks and imagined that both arose from an undifferentiated inner layer of the "archiplacophoran" plates. The shell of the Conchifera became univalved he believed by fusion of the shell and shell fields. There is no evidence, however, that the dynamics involved in the process of earliest shell deposition through the interplay of shell-field invagination and pellicle in Conchifera could have evolved from the very different process of shell-plate production found in chitons.

Thus, recent work on the ontogeny and structure of shell in chitons and Conchifera shows such major differences between them that it can be questioned whether there was a monophyletic origin of molluscan shell, or rather one origin for chitons and a second for the remaining extant and extinct Conchifera. Tubules in the shells of the monoplacophoran *Neopilina* (Schmidt, 1959), bivalves (e.g. Waller, 1980), and gastropods have sometimes been considered homologous with the aesthete canals of chitons and argued as a support for a monophyletic origin of molluscan shell (e.g. Salvini-Plawen, 1985), but the homology is so far uncertain. When the ontogenetic development of *Neopilina* becomes known, perhaps a basis will be found for deciding whether molluscan shell has a monophyletic or polyphyletic origin.

### CHAETODERM ORAL SHIELD AND THE ARCHIMOLLUSK

One of the original arguments for dividing the Aplacophora into two classes and, ultimately, into two subphyla depends on the hypothesis that mollusks have a turbellariomorph, or flatworm, ancestry. This phylogeny is based on a supposed homology and similarity in mode of locomotion between mollusks and flatworms by means of a "ventral mucociliary gliding surface" (Salvini-Plawen, 1972, 1980: Fig. 5, 1985; see also Trueman, 1976). The molluscan archetype, like the flatworms, is said not to possess a separation of the head from the foot, and the mouth consequently opens through the sole; innervation of the sole is said to be from both the cerebral ganglia and ventral nerve cord. [Stasek (1972) has illustrated but not discussed a head separate from the locomotory sole in the turbellariomorph molluscan precursor.]

Support for the flatworm-like archimolluscan locomo-

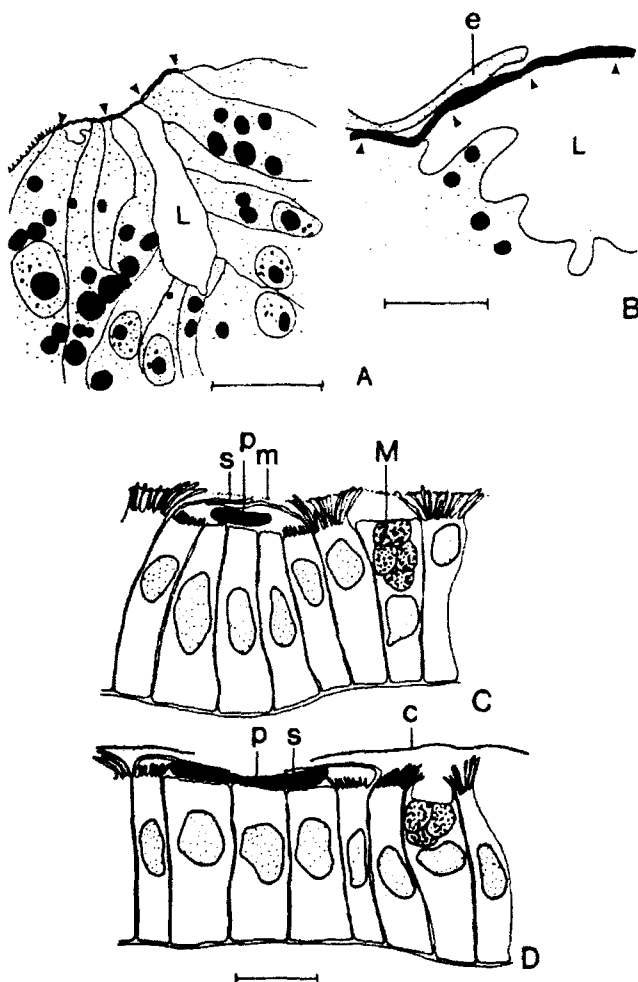


Fig. 4. Larval shell deposition in (A, B) the gastropod *Aolidia papillosa* (Linnaeus) and (C, D) the chiton *Ischnochiton rissoi* (Payaudreau). In A, an organic pellicle (arrows) covers the lumen of the shell field invagination (L); in B, the edge of the pellicle can be seen to be overlain by a cytoplasmic extension (e). Calcium carbonate has not yet been deposited. (Drawn after photographs in Eyster and Morse, 1984: Figs. 1, 2). In C, calcium carbonate of the shell plate (p) has been deposited under the overlapped microvilli (s, "stragulum"); a mucus layer (m) covers the stragulum. In D, microvillar processes (s) have pulled apart and a cuticle (c) with a contrasted outer layer is beginning to form; M is perhaps a mucus cell (C and D after Kniprath, 1980.) Scale bars: A = 10  $\mu$ m; B = 0.5  $\mu$ m; C; D approximately 6  $\mu$ m.



tory ventral surface is said to be shown by the cerebrally innervated oral shield of the burrowing Chaetodermomorpha (= Caudofoveata) (Fig. 6A); that is, the shield is regarded as a remnant of the original gliding surface (Salvini-Plawen, 1972, 1980, 1985). The homology with a creeping sole was originally based on histologic similarities in the morphology and arrangement of nerve and mucous cells that lie in the epidermis beneath the oral shield cuticle of chaetoderms and the spiculeless cuticle within the foot-furrow of the creeping neomeniomorphs [Hoffman, 1949; for a translation and explanation, see Scheltema (1983)]. The homology, however, is spurious since molluscan ectoderm, with or without cuticle, is richly supplied with both nerve and mucous cells. Furthermore, Salvini-Plawen (1985) has described (but not illustrated) the specialized ultrastructure of the oral shield, consisting of interdigitated microvilli with glycocalyxes and supporting fibers.

The oral-shield cuticle and epithelium in six genera (*Scutopus*, *Limifossor*, *Prochaetoderma*, *Metachaetoderma*, *Falcidens*, and *Chaetoderma*) representing all families of chaetoderms are continuous with pharyngeal (oral tube) cuticle and epithelium (Scheltema, 1981, 1983). Light microscopy does not reveal a border where the oral shield cuticle joins the pharyngeal cuticle (Figs. 5, 6B), but ultrastructural studies would define this area better. *Scutopus* is considered to be the most primitive chaetoderm because of its least differentiated midgut (Scheltema, 1981) and because of the evidence of ventral fusion of the cuticle (Salvini-Plawen, 1972). In this genus only scattered pyriform mucous cells open through the



Fig. 5. Oral shield of a Chaetodermomorpha: section through the mouth, pharynx, and oral shield of *Scutopus megaradulatus* Salvini-Plawen showing continuous cuticle of pharynx and oral shield (from 650 m off Cape Hatteras, North Carolina, U. S. A., 34°14.8'N, 75°46.7'W; fixed in formalin, preserved in alcohol, stained with haematoxylin/Gray's double contrast, sectioned at 0.7  $\mu$ m.) (c, spiculose cuticle of integument; n, nerve fibers from precerebral ganglion; o, cuticle of oral shield; p, cuticle of pharynx). Small arrow indicates change from oral shield cuticle with a thickened outermost layer to homogeneous cuticle of pharynx. Scale bar = 0.05 mm.

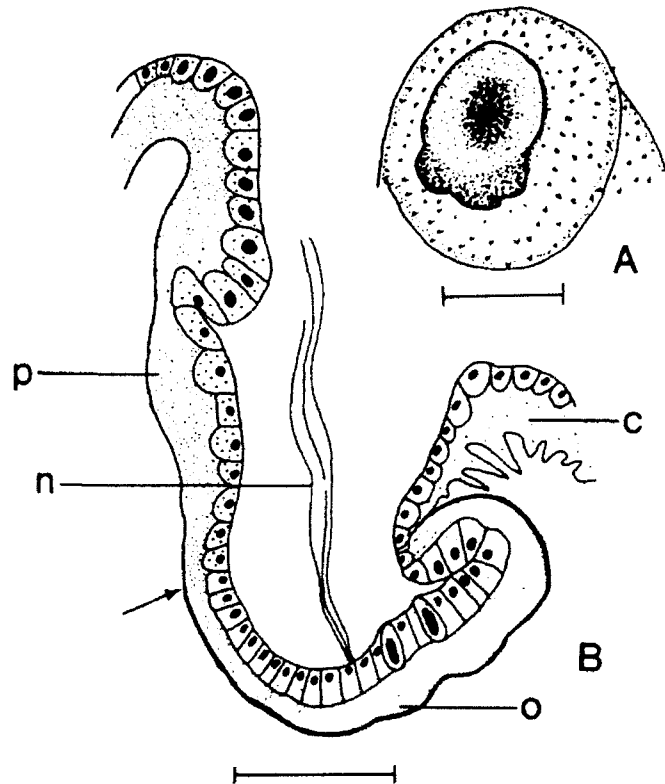


Fig. 6. Oral shield of *Scutopus megaradulatus*. A. Anterior view of oral shield *in situ* surrounding darkened mouth in center. B. Semischematic drawing of area between large arrowheads in figure 5 showing histology of pharyngeal and oral shield cuticle (lettering and small arrow as in Fig. 5). Scale bars: A = 0.3 mm; B = 0.05 mm.

oral shield, further refuting Hoffman's homology, which likened the lobes of mucous cells opening at the lateral edges of the oral shield in advanced Chaetodermatidae with the pedal gland of Neomeniomorpha. This important aspect of Hoffman's homology linking lobed mucous cells of the oral shield and foot furrow was ignored by Salvini-Plawen (1980) while retaining the homology itself. Definitive evidence that the oral shield is a part of a vestigial ventral sole would require innervation from the ventral (= pedal) nerve cord rather than from the cerebral ganglia.

Thus, the oral shield of the Chaetodermomorpha is considered here to be an autapomorphy, a cerebrally innervated external continuation of pharyngeal cuticle like a lip belonging to the head, not to a ventral sole. There is no convincing evidence that it is a remnant of an original creeping sole homologous to the ventral surface of a turbellarian flatworm. The separation of the Aplacophora into two classes based on the supposed (1) plesiomorphy of ventral innervation of the chaetoderm oral shield by the cerebral ganglia and (2) apomorphy of a head separate from the foot in the neomenioids and all other mollusks except chaetoderms is unsatisfactory. A head separate from the foot is considered here to be a plesiomorphy shared by mollusks generally but lost in the bivalves and, because of their burrowing habit, also in the chaetoderms.

## RADULA

### APLACOPHORAN RADULA

Evidence from the radula morphology of aplacophorans and from the ontogeny of gastropod and chiton radulae suggests that the molluscan radula originated as a paired structure.

The radula in chitons, the monoplacophoran *Neopilina*, gastropods, and scaphopods is a chitinous structure formed of a single continuous ribbon, or radular membrane, which bears serial rows of teeth; both ribbon and teeth are continually secreted at the proximal end of a pharyngeal diverticulum, the radular sac (Fretter and Graham, 1962; Kerth, 1983; Scheltema, unpub. data). Each row of teeth has left and right sides and usually a central, or median, tooth. The radula is bilaterally symmetrical around the central tooth, that is, the

teeth of each side are mirror images of one another. Along the length of the ribbon each tooth has the same shape as the tooth in front of and behind it, that is, the rows of teeth are serially repeated.

In the Aplacophora, the radula is formed in the usual manner and is likewise bilaterally symmetrical and serially repeated (Figs. 7A, 8A, C). The radula has been called monostichous or monoserial if there is only a single tooth in a row; with two mirror-image teeth in each row, distichous or biserial; and with more than two mirror-image teeth, polystichous or polyserial (Nierstrasz, 1905).

The usual type of radula in the Aplacophora is distichous; a central tooth is lacking in nearly all species. Unique among mollusks the radular membrane itself is divided down the middle so that the entire radula is a bipartite, bilaterally symmetrical, serial structure consisting of two strips

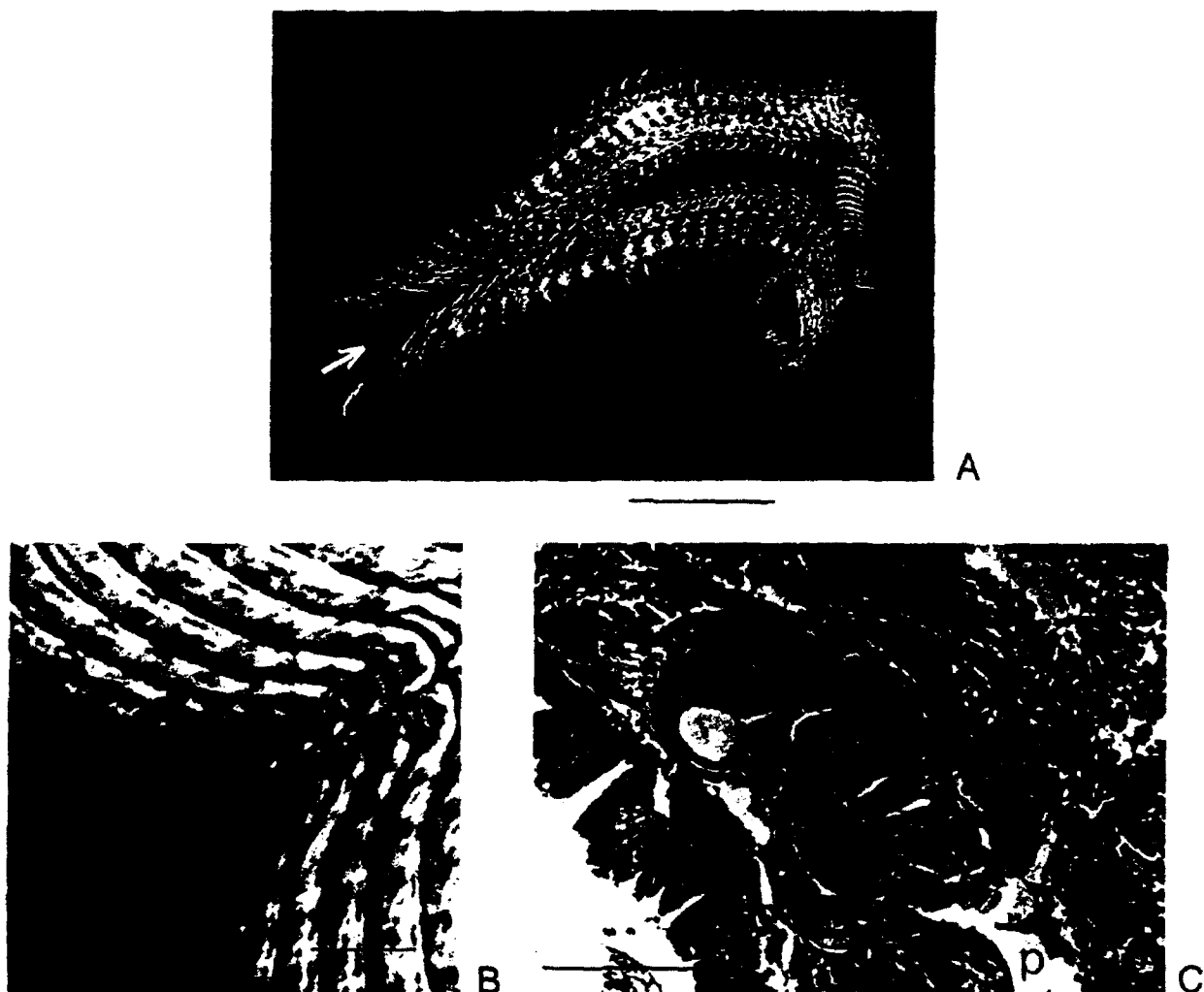


Fig. 7. Aplacophoran radula of *Simrothiella* species. A. *Simrothiella* sp. b (undescribed); at left are the newest, proximal teeth and fused radular membrane (arrow); distally (on the right) the membrane is bipartite and spirals ventrally down into two ventral pharyngeal pockets. B. Close-up of fused, proximal end of radula shown in A. (Whole amount in glycerine; see Scheltema, 1981, for dissecting technique). C. *Simrothiella* sp. a (undescribed), sagittal section through one side of radula, indicated by single arrowheads; double arrowheads show radula within the ventral pharyngeal pocket (Specimens from 2,633 m at 20°50'N, 109° 0.6'W; sections treated as in Fig. 5). Scale bars: A = 100  $\mu$ m; B = 30  $\mu$ m; C = 100  $\mu$ m.

of continuous ribbon, each strip with rows of single denticulate teeth which are the mirror image of the opposed teeth (Figs. 7A, 8A, C). The two parts of the radular membrane are fused to a greater or lesser extent lengthwise along their medial (inner) edges forming a one-piece, unipartite radular ribbon along part of its length (Figs. 7B, 8A; Scheltema, 1981).

The structure of the radula is clear only when it is dissected and isolated from surrounding tissue (Scheltema, 1981). Reconstructions from histologic sections have resulted

in misconceptions of actual structure and probable modifications during its evolution [e.g. Nierstrasz, 1905; Salvini-Plawen, 1972, 1978 (*Simrothiella*), 1985].

In order to differentiate the two states that exist for the radular membrane among mollusks, the terms "bipartite" and "unipartite" are used here, and the terms using "—stichous" are reserved for descriptions of the radular teeth only. Thus, a distichous radula can be either uni- or bipartite, but a monostichous radula is necessarily unipartite. The terms with "—serial," which should mean "arranged in series," are not used here, thus obviating the confusion of such a description as "monoserial with paired teeth."

As in other radulate Mollusca, the radular membrane in Aplacophora appears to migrate forward as teeth are added by the odontoblasts; in most species the membranes turn anteroventrally into paired or unpaired ventral pharyngeal pockets, where dissolution of the radula apparently occurs (Figs. 7C, 8D). Unlike grazing gastropods and chitons, in all but one family of Aplacophora the teeth show no wear and thus do not rasp.

The entire radula of juvenile specimen of *Simrothiella* (0.9 mm in length) has been examined. Within each ventral pharyngeal pocket is preserved the earliest ontogenetic development; the first tooth is a nondenticulate bar on a wide expanse of radular membrane (Fig. 8B). As the radula grows in length and width, denticles are added to the teeth medially, i.e. at their inner edges (Fig. 8A). Histologic cross-sections through the proximal, blind end of the radular sac show odontoblasts in two discrete groups, each presumably bound by basement membrane (Figs. 9, 10). The two groups lie within a single sac, surrounded in the usual manner by muscle.

Within the Aplacophora, the radula has evolved at least twice from having a bipartite, distichous radula (Figs. 7, 8) to a radula with a unipartite radular membrane. In the Dondersiidae (Fig. 11), the radula is altogether absent or consists of

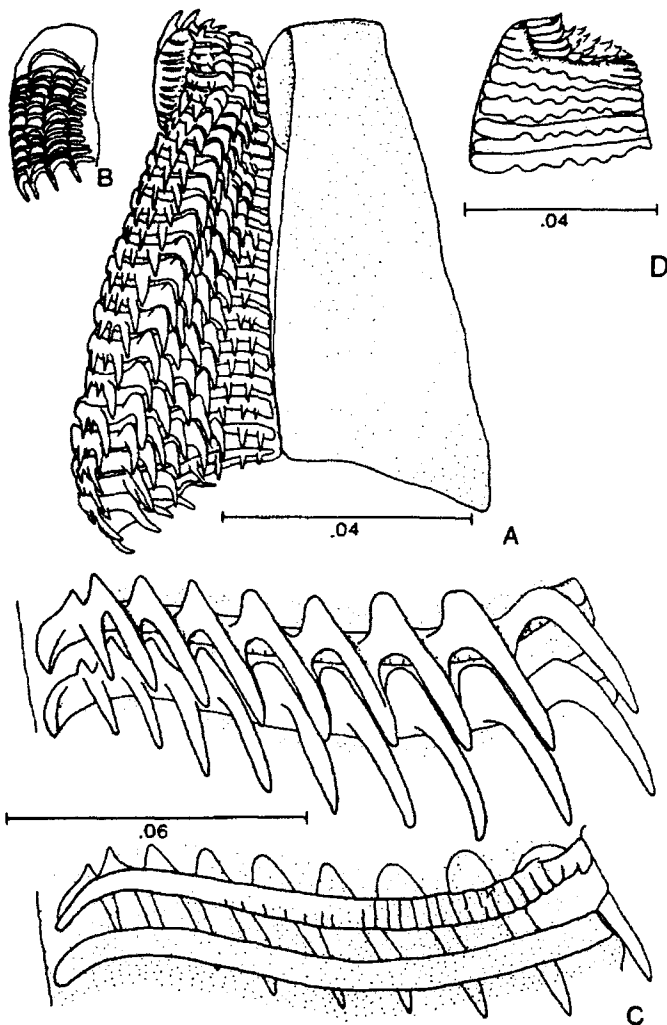


Fig. 8. Radula of *Simrothiella* sp. b (undescribed), radular membrane indicated by stippling. A. Entire radula of a juvenile specimen, dorsal view, anterior (oldest teeth) at top. Teeth of only left half of radula shown; teeth on the right are the mirror-image of those on the left. Denticles are added to the teeth medially as the radula widens and lengthens. B. Distal, oldest part of left radular strip shown folded under in A from ventral pharyngeal pocket; original, first-formed tooth is retained. C. Two views of the same two adjacent teeth from an adult specimen: upper teeth drawn in dorsal view as if they were on the right side of the radula, medial denticles on left; lower teeth from left side of radula drawn from beneath radular membrane. D. Most anterior part of the same adult radula from which teeth in C were drawn; comparison with juvenile radula B indicates that there is dissolution at the distal end of the radula within the ventral pharyngeal pocket (Specimens from 2,633 m at 20°50'N, 109°06'W). Scale bars in mm.



Fig. 9. Radular sac of *Simrothiella* sp. a (undescribed). Anterior view of somewhat oblique cross-section through proximal end showing membranes (arrowheads) bounding right and left groups of radula secretory cells (Specimen from 2,633 m at 20°50'N, 109°06'W). Scale bar = 35  $\mu$ m.

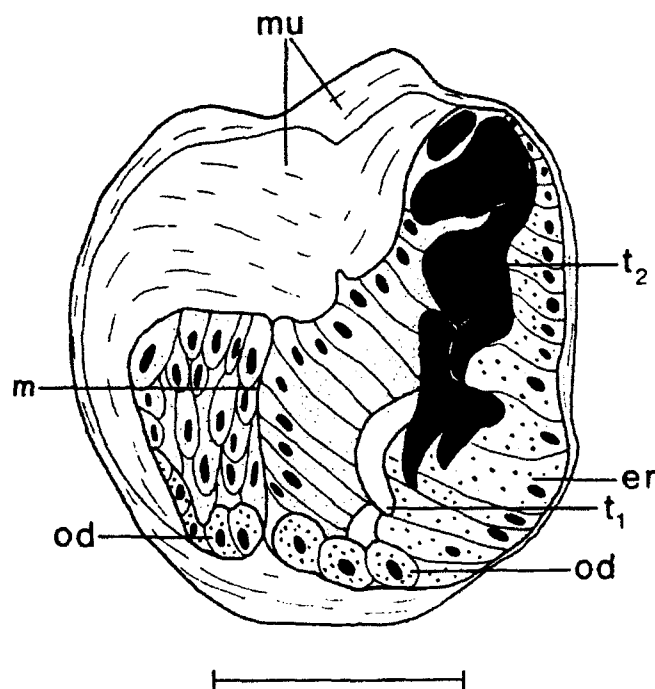


Fig. 10. Semischematic representation of radular sac cross-section shown in figure 9 (er, epithelium of radular membrane; m, membranes bounding left and right groups of radula secretory cells; mu, muscle; od, odontoblasts;  $t_1$ , early tooth, or perhaps denticle, not yet staining with haemotoxylin;  $t_2$ , older tooth stained by haemotoxylin). Scale bar = 35  $\mu$ m.

only a few rows of single teeth, usually 6 or fewer. Its monostichous form appears to be the result of reduction and fusion of a distichous radula, with two of its paired denticles fused at tip and base. In the Prochaetodermatidae, the radula has evolved into a rasping structure with a unipartite radular membrane and a central tooth, or plate (Fig. 12) (Scheltema, 1981,1985).

There are no distinctive radula characteristics, synapomorphies, held in common or uniquely by the Aplacophora and Polyplacophora, the latter with rows of usually 17 teeth on a unipartite radular membrane.

#### ONTOGENY OF GASTROPOD AND CHITON RADULAE

Vestiges of an original distichous molluscan radula exist in the ontogenetic development of the chiton, pulmonate, opisthobranch, and prosobranch radula. The details of the developing chiton radula are treated by Eernisse and Kerth (1987) and Kerth (this symposium). The radula starts as rarely one to usually three pairs of lateral teeth on a unipartite radular membrane with a central tooth added later. In the ontogenetic development in five families and seven species of pulmonates, the radula begins as a distichous structure with two longitudinal rows of lateral teeth on a unipartite radular membrane; further laterals are then added, and finally a central tooth, which originally may be paired, is secreted thereby uniting the cross-rows (Kerth, 1979). Pruvot-Fol (1926) figured the earliest radular teeth of the opisthobranch *Polycera*,

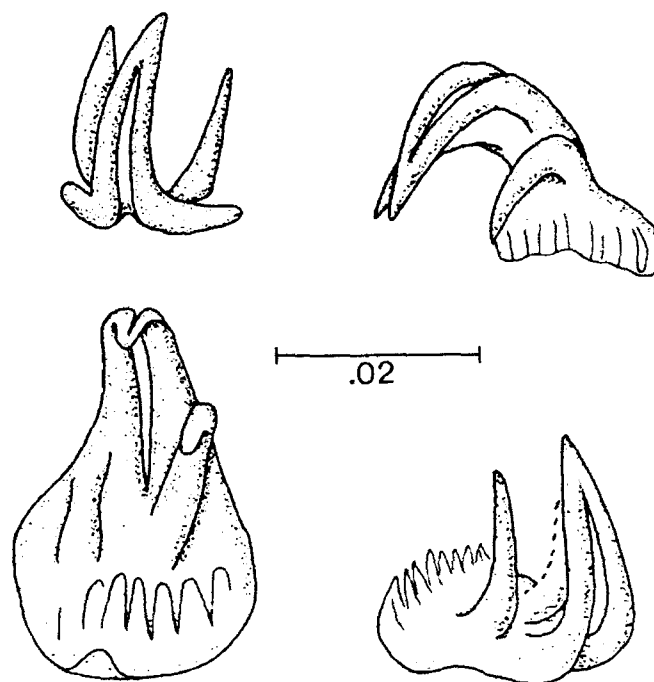


Fig. 11. Monostichous aplacophoran radula of an undescribed species of Atlantic Dondersiidae, four aspects; radular membrane not shown. One denticle is missing from the teeth in the lower two drawings (Specimen from 805 m, 39°51.3'N, 70°54.3'W). Scale in mm.



Fig. 12. Undivided, unipartite radular membrane of an undescribed species of Prochaetodermatidae; view of ventral surface (Specimen from 1,624 m 10°30.0'N, 17°51.5'W). Scale = 250  $\mu$ m.

distichous with a "gouttiere" between them. The radular sac in the opisthobranch *Rhodope* (Riedl, 1960) and in the pulmonate *Physa* (Wierzejski, 1905) originates as a pair of invaginations. In *Rhodope*, lacking a radula, the paired invaginations are lost; in *Physa*, they unite to form a single sac. The developing radular sac in prosobranchs is often bifid (Fretter and Graham, 1962: 173).

To summarize, the most generalized aplacophoran radula is unique because it has a bipartite radular membrane with distichous teeth. Distichous teeth on a unipartite radular membrane exist ontogenetically in other molluscan groups.

### PERICARDIUM

The pericardium is a space lined by mesoderm arising embryologically from cell 4d; therefore, it may be considered to be coelom. Raven (1966) questioned, however, whether coelomic cavities among mollusks arise from mesodermal bands (schizocoels) as they do among the annelids. [For an extensive overview of gonopericardial complexes within mollusks, see Wingstrand (1985)].

Salvini-Plawen (1968) hypothesized that the pericardial space evolved within the mesenchyme after the heart, surrounding it and thereby improving its function. Stasek (1972: Fig. 1A, B) illustrated such a situation in the molluscan precursors. Although the pericardium is relatively small in most gastropods and bivalves, in the three primitive classes Aplacophora, Monoplacophora, and Polyplacophora it is spacious relative to the size of the heart (Fig. 13). In *Neopilina* the pericardium is paired, and in the aplacophoran *Chaetodermomorpha* and most *Neomeniomorpha* it has either small or large, paired lateral extensions ("horns" in early literature), whose function is not known. Ontogenetically, in the single species of aplacophoran for which size during development is mentioned (Baba, 1938), the pericardium is already large before the heart develops.

How the pericardium functionally could have evolved in a pre-mollusk as a small space, then have become spacious and probably paired, and finally again become reduced in size, is difficult to imagine. Moreover, during organogenesis, the pericardium develops before the heart and the heart arises

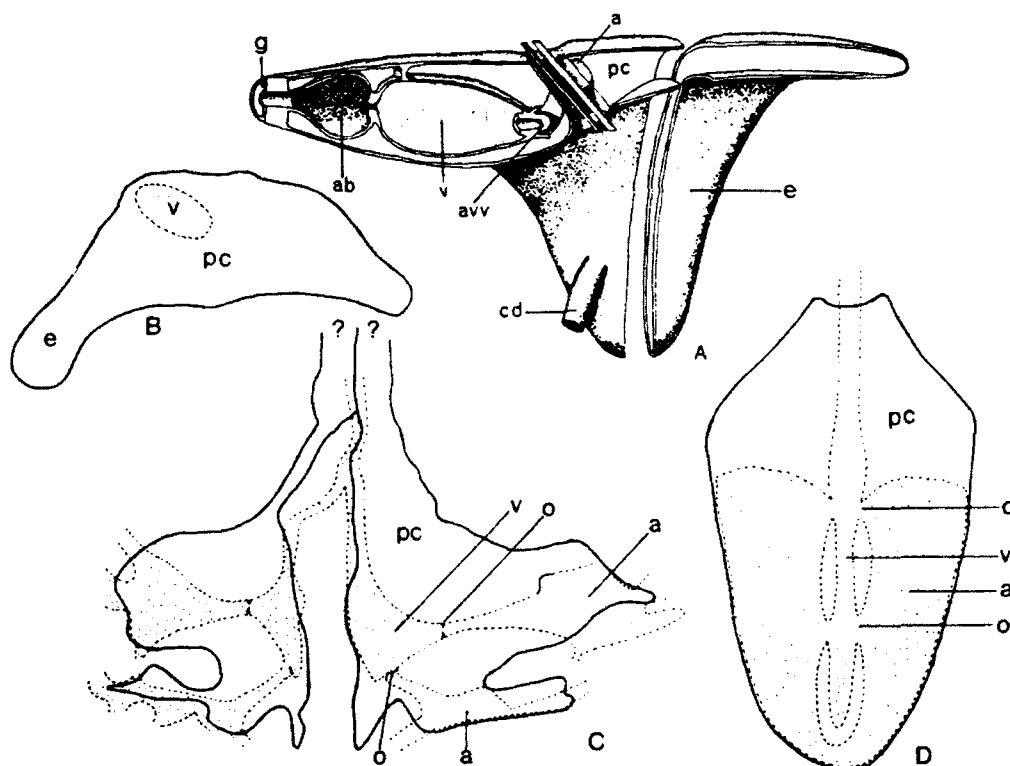


Fig. 13. Heart and pericardium in the primitive molluscan classes Aplacophora (A, B), Monoplacophora (C), and Polyplacophora (D) showing large pericardial spaces in relation to the size of the heart. In B, C, and D the heart is stippled and the pericardium is blank. A. *Chaetoderma nitidulum* Lovén, sagittal section through pericardium, heart, and gonopericardial duct (after Scheltema, 1972). Paired auricles (a) open into the ventricle on each side of an atrioventricular valve (avv). Gonads empty through paired ducts (g) into the pericardium (pc), and coelomoducts (cd) lead from the pericardium to the cloaca (not shown). The large paired lateral extensions of the pericardium (e) are known as "horns" in the older literature. B. *Simrothiella* sp. a (original drawing), same specimen as in figure 9. Somewhat oblique cross-section through the pericardium (pc), ventricle (v), and lateral extension of the pericardium (e). C. *Neopilina galathea* Lemche, dorsal view (after Lemche and Wingstrand, 1959). The pericardium (pc) and ventricles (v) are paired; two pairs of auricles (a) open into each ventricle. It is not known whether there is a connection between the pericardia and gonads (see Wingstrand, 1985). D. *Acanthopleura echinata*, dorsal view (after Plate, 1898). Two pairs of ostia (o) open on each side into the ventricle (v); the number of ostia varies from one to four pairs, according to species (a, auricle; ab, aortal bulb; avv, atrioventricular valve; cd, coelomoduct; e, lateral extension of pericardium; g, gonopericardial duct; o, opening between auricle and ventricle; pc, pericardium; v, ventricle). Scales not indicated.

from the dorsal or inner epithelium of the pericardium (Baba, 1938; Raven, 1966), suggesting that evolution of the pericardium probably preceded that of the heart. The large pericardial spaces in the Aplacophora, Monoplacophora, and Polyplacophora point to a coelomate rather than to an acoelomate, turbellariomorph ancestor and lead one to re-examine the evidence for ancestral relationship between the annelids and mollusks (see Vagvolgyi, 1967; Wingstrand, 1985).

## DISCUSSION

### ACOELOMATE VERSUS COELOMATE MOLLUSCAN ORIGINS

The hypothesis that the ancestor of mollusks was acoelomate is rejected in favor of a coelomate origin because: (1) primitive molluscan taxa have large pericardial spaces; (2) evidence is lacking that the pericardial space began as a small opening in mesenchyme lined by mesoderm; (3) Wingstrand's evidence (1985) strongly suggests a molluscan "derivation from advanced oligomeric *Spiralia* ('proto-annelids' or 'proto-articulates')" (p. 8) (Fig. 14).

The existence of large pericardial spaces in the primitive extant mollusks has not been considered in hypotheses of an acoelomate molluscan origin. Rejection of the hypothesis of reduced metamerism as the origin of molluscan coelom is probably correct (Salvini-Plawen, 1968); however, one need not suppose, therefore, a total absence of either coelom or metamerism. Reiger (1985), after careful comparative studies of the fine structure of acoel connective tissue, argued that the acoelomate Bilateria themselves are derived through progenesis from a coelomate ancestor.

### SHELL AND SPICULES

The Aplacophora probably evolved from a shell-less rather than from a shelled ancestor. Evidence for this assertion comes from properties of the cuticle (see SHELL AND SPICULES above) and from a comparison of numbers of dorsoventral muscles that run between the outer body wall and foot among various mollusks. In the Neomeniomorpha, two bilateral sets of oblique bands are repeated serially along the body; they are considered homologous to the dorsoventral pedal muscles in other mollusks (Salvini-Plawen, 1972). The evolution of dorsoventral musculature, which coevolved with the shell, has been toward reduction in number, from eight in Polyplacophora and tryblidian Monoplacophora to one in most Gastropoda. The serial arrangement of numerous bands in the Neomeniomorpha is considered therefore to be a plesiomorphy that preceded shell development and its consequent reduction of dorsoventral musculature.

No convincing published evidence links the process of extracellular spicule formation by a single cell (Haas, 1981) with the development of shell fields and shell deposition. The only common attribute of spicule and shell formation is that both are extracellular deposits of calcium carbonate.

Three types of calcium carbonate coverings are found in the Mollusca: spicules in Aplacophora and Polyplacophora; the shell plates of the Polyplacophora with a thin

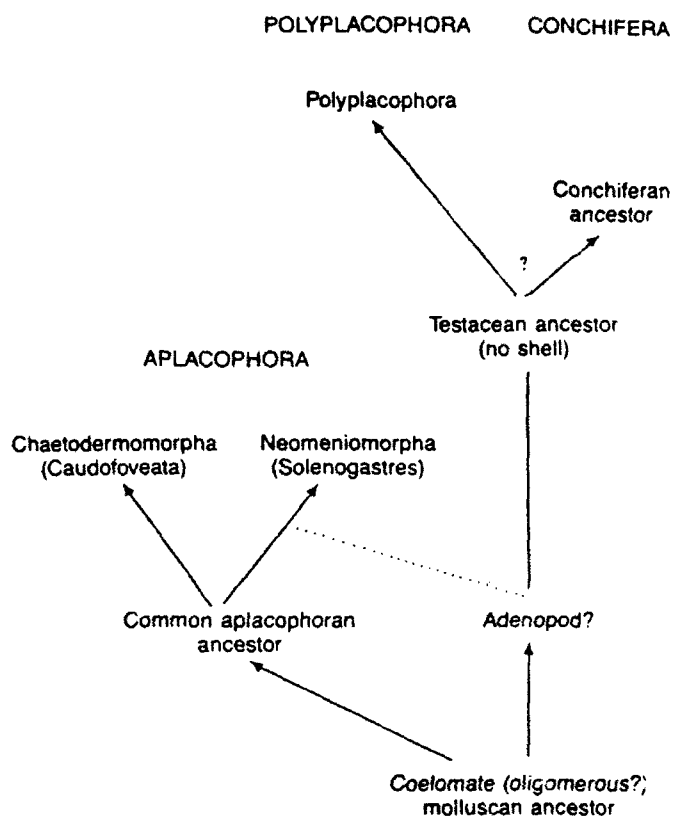


Fig. 14. Phylogeny of the Mollusca (adapted from Wingstrand, 1985). The questioned Adenopod can be dropped (see argument in section "Chaetoderm oral shield and the archimollusk"). The text raises questions about a common testacean ancestor in comparing chiton and conchiferan shell formation and structure (see argument in section "Shell and Spicules"). A coelomate molluscan ancestor, whether or not oligomorous, is corroborated here (see section "Pericardium"). A common aplacophoran ancestor descended directly from the stem mollusk is indicated (see sections "Chaetoderm oral shield and the archimollusk" and "Aplacophora, a monophyletic group"). The stem mollusk had a paired radula with a two-part radular membrane and distichous teeth (see section "Radula").

(nonperiostracal) organic cover, tegmentum, and hypostracum; and the conchiferan shell with periostracum, prismatic layer, and nacreous layer. The trend has been to treat these calcium carbonate structures as homologous, with a morphocline leading from spicules to plates by coalescence in chitons (e.g. Salvini-Plawen, 1972), and from the 8 shell fields in chitons to the single shell field of univalves and bivalves (e.g. Haas, 1981). From the evidence of structure and ontogeny, and discounting the problematic "Pruvot's larva," the existence of this morphocline is seriously questioned.

Is there a single ancestor for polyplacophorans and the remaining shelled mollusks? Wingstrand (1985) makes a strong case for such a hypothetical testacean ancestor, equivalent to the archiplacophoran of figure 1, based on synapomorphies of radula with its supports and musculature, oral flaps, digestive system, pharyngeal diverticula, 8 pairs of pedal retractors, and, possibly, the number and position

of atria (Fig. 13). The shells in chitons are considered to be autapomorphies, but the shell fields and the mineralization process are homologous and monophyletic in chitons and Conchifera. Reasons have been stated above (section on Shell and Spicules) for doubting this homology (Fig. 14). Answers to questions about Puvion's larva and the relationship of polyplacophoran plates to conchiferan shells could lie in the unknown embryology of *Neopilina* and with the yet-to-be reexamined Puvion's larva.

## RADULA

The direction of evolutionary change in the structure of the aplacophoran radula appears to be from a paired, or bipartite, radular membrane to a single, unipartite ribbon. The rationale for this polarity is based on several points. (1) Rasping seems a more advanced, complicated function for a radula over a simple ability to grasp as found in most Aplacophora. Rasping probably requires the integration of structure provided by a unipartite radular membrane. Only among the Prochaetodermatidae is there wear of the anterior teeth, i.e. evidence of rasping (Schelte, 1981, 1985), and here the radular membrane is also unipartite. (2) All other radulate aplacophorans except the Dondersiidae and Chaetodermatidae with reduced and specialized teeth (Fig. 11, Schelte, 1972) have a bipartite radular membrane with a fused, unipartite section that often retains visible evidence of fusion; the region of this fused section is not fixed but varies among families and genera (Schelte, 1981). It is possible, but not parsimonious, to imagine that the radular membrane was originally unipartite, then divided into two, and finally fused again; however, if so, the odontoblasts producing such a secondarily derived, paired radula would have to evolve from a single into a paired group of cells. (3) During ontogeny of the radula in chitons and gastropods, the central tooth is added only after several rows of one or more pairs of lateral teeth have been formed. Presumably the median part of the ribbon is where an originally paired ribbon became unified; subsequently odontoblasts for the central tooth could come into being.

The paired structure of the aplacophoran radula is considered to be the primitive form in mollusks because the direction of evolution, distichous bipartite to distichous unipartite in Aplacophora, is continued in the ontogeny of the gastropod radula, from distichous unipartite to polystichous. Since aplacophorans probably evolved from a shell-less ancestor (see above), the distinctive molluscan structure of a radula was already present when shell evolved (Fig. 14). The aplacophoran plesiomorphic bipartite radula does not form a basis for linking the Aplacophora closely to any other taxon of mollusks.

## APLACOPHORA, A MONOPHYLETIC GROUP

The Aplacophora should not be separated into two classes or subphyla on the erroneous homology of the chaetoderm oral shield with a turbellariomorph creeping sole. The oral shield is an autapomorphy of the Chaetodermomorpha. The Neomeniomorpha and Chaetodermomorpha form a monophyletic group with the following probable synapomorphies: a rounded worm shape; a dorsoterminal sen-

sory organ [a chemoreceptor lying external to the mantle cavity, and not known to be ontogenetically or functionally homologous to the osphradium within the mantle cavity of other mollusks (Haszprunar, 1987)]; three to six pairs of precerebral ganglia or swellings (Salvini-Plawen, 1978, 1985), a reproductive system in which the gonads empty into the pericardium through gonopericardial ducts and the pericardium is emptied into the cloaca through coelomoducts (Fig. 13A) (but see Salvini-Plawen, 1972, 1985). An adenopod ancestor becomes a superfluous construct (Fig. 14). As the direction of evolution of organ systems within the Aplacophora becomes clear, new insights into the evolution of mollusks should come to light.

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## LITERATURE CITED

- Baba, K. 1938. Later development of a Solenogastre, *Epimeda verrucosa* (Niestrasz). *Journal of the Department of Agriculture, Kyusyu Imperial University* 6:21-39.
- Beedham, G. E. and E. R. Trueman. 1968. The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. *Journal of Zoology* 154:443-451.
- Boss, K. J. 1982. Mollusca. In *Synopsis and Classification of Living Organisms*, S. P. Parker, ed., pp. 945-1165. McGraw-Hill, New York.
- Eernisse, D. J. and K. Kerth. 1988. The initial stages of radular development in chitons (Mollusca: Polyplacophora). *Malacologia* 29:95-103.
- Eyster, L. S. and M. P. Morse. 1964. Early shell formation during molluscan embryogenesis, with new studies on the surf clam, *Spisula solidissima*. *American Zoologist* 24:871-882.
- Fischer, F. P. 1988. The ultrastructure of the aesthetes in *Lepidopleurus cajetanus* (Polyplacophora, Lepidopleurina). *American Malacological Bulletin* 6(1):153-159.
- Fischer, F. P., W. Maile and M. Renner. 1980. Die Mantelnapfien und Stacheln von *Acanthochiton fasciculans* L. (Mollusca, Polyplacophora). *Zoomorphologie* 94:121-131.
- Fretter, V. and A. Graham. 1962. *British Prosobranch Molluscs*. Ray Society, London. 755 pp.
- Grégoire, C. 1972. Structure of the molluscan shell. In *Chemical Zoology Vol. 7 Mollusca*, M. Florin and B. T. Scheer, eds., pp. 45-102. Academic Press, New York and London.
- Haas, W. 1977. Observations of the shell and mantle of the

- Placophora. In: *The Mechanisms of Mineralization in Invertebrates and Plants*, N. Watabe and K. W. Wilbur, eds. pp. 389-402, Belle W. Baruch Library in Marine Science.
- Haas, W. 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia* 21:403-418.
- Haas, W., K. Kriesten and N. Watabe. 1980. Preliminary note on the calcification of the shell plates in chiton larvae (Placophora). In: *The Mechanisms of Biomineralization in Animals and Plants*, M. Omon and N. Watabe, eds. pp. 67-72. Tokai University Press, Tokyo.
- Hadfield, M. G. 1979. Aplacophora. In: *Reproduction of Marine Invertebrates*, Vol. 5, A. C. Giese and J. S. Pearse, eds. pp. 1-25. Academic Press, New York.
- Haszprunar, G. 1987. The fine morphology of the osphradial organs of the mollusca. IV. Caudoloveata and Solenogastres. *Philosophical Transactions of the Royal Society of London B* 315:63-73.
- Hoffman, S. 1949. Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. *Zoologische Beiträge von Uppsala* 27:293-427.
- Hyman, L. H. 1967. *The Invertebrates. Mollusca I*, Vol. VI, McGraw-Hill, New York, 792 pp.
- Kerth, K. 1979. Phylogenetische Aspekte der Radulamorphogenese von Gastropoden. *Malacologia* 19:103-108.
- Kerth, K. 1983. Radulaapparat und Radulabildung der Mollusken. I. Vergleichende Morphologie und Ultrastruktur. *Zoologische Jahrbücher für Anatomie* 110:205-237.
- Kniprath, E. 1980. Ontogenetic plate and plate field development in two chitons, *Middendorffia* and *Ischnochiton*. *Wilhelm Roux's Archives of Developmental Biology* 189:97-106.
- Kniprath, E. 1981. Ontogeny of the molluscan shell field: a review. *Zoologica Scripta* 10:61-79.
- Kowalevsky, M. A. 1883. Embryogénie du *Chiton polii* Phil., avec quelques remarques sur le développement des autres Chitons. *Annales de la Musée d'Histoire Naturelle de Marseille* 1:1-46.
- Lemche, H. and K. G. Wingstrand. 1959. The anatomy of *Neopilina galathea* Lemche, 1957 (Mollusca Tryblidiacea). *Galathea Report* 3:9-71.
- Nierstrasz, H. F. 1905. *Kruppomenia minima* und die Radula der Solenogastren. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 21:655-702.
- Pearse, J. S. 1979. Polyplacophora. In: *Reproduction of Marine Invertebrates*, Vol. 5, A. C. Giese and J. S. Pearse, eds. pp. 27-85. Academic Press, New York.
- Plate, L. H. 1898. Die Anatomie und Phylogenie der Chitonen. *Zoologische Jahrbücher Suppl. IV. (Fauna Chilensis I)*: 1-243.
- Poulicek, M. and B. Kreusch. 1983. Evolutionary trends in skeletal structures of Polyplacophora. In: *Proceedings of the 8th International Malacological Congress*, L. Pinter, ed. pp. 207-212. Hungarian Natural History Museum, Budapest.
- Pruvot, G. 1890. Sur le développement d'un Solénogastre. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences* 111:689-692.
- Pruvot-Fol, A. 1926. Le bulbe buccal et la symétrie des mollusques. 1. La radula. *Archives de Zoologie expérimentale et générale* 65:209-343.
- Raven, C. P. 1966. *Morphogenesis: The analysis of molluscan development*. Pergamon Press, Oxford. 365 pp.
- Riedl, R. 1960. Beiträge zur Kenntnis der *Rhodope veranii*, Teil II. Entwicklung. *Zeitschrift für wissenschaftliche Zoologie* 163:237-316.
- Rieger, R. M. 1985. The phylogenetic status of the acoelomate organization within the Bilateria: a histological perspective. In: *The Origins and Relationships of Lower Invertebrates*, S. Conway Morris, J. D. George, R. Gibson and H. M. Platt, eds. pp. 101-122. Systematics Association Special Vol. 28, Clarendon Press, Oxford.
- Rolle, W. D. J. 1981. *Septemchiton* - a misnomer. *Journal of Paleontology* 55:675-678.
- Runneger, B. and J. Pojeta, Jr. 1985. Origin and diversification of the Mollusca. In: *The Mollusca*, Vol. 10, Evolution, E. R. Trueman and M. R. Clarke, eds. pp. 1-57. Academic Press, Inc. Orlando.
- Salvini-Plawen, L. von. 1968. Die 'funktions-coelom theorie' in der evolution der Mollusken. *Systematic Zoology* 17:192-208.
- Salvini-Plawen, L. von. 1972. Zur Morphologie und Phylogenie der Mollusken. Die Beziehungen der Caudoloveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Zeitschrift für wissenschaftliche Zoologie* 184:205-394.
- Salvini-Plawen, L. von. 1978. Antarktische und subantarktische Solenogastres (eine Monographie 1898-1974). *Zoologica (Stuttgart)* 44:1-315.
- Salvini-Plawen, L. von. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* 19:249-278.
- Salvini-Plawen, L. von. 1985. Early evolution and the primitive groups. In: *The Mollusca*, Vol. 10, Evolution, E. R. Trueman and M. R. Clarke, eds. pp. 59-150. Academic Press, Inc. Orlando.
- Schellema, A. H. 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere* 72:361-370.
- Schellema, A. H. 1973. Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere* 76:97-107.
- Schellema, A. H. 1978. Position of the class Aplacophora in the phylum Mollusca. *Malacologia* 17:99-109.
- Schellema, A. H. 1981. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia* 20:361-383.
- Schellema, A. H. 1983. On some aplacophoran homologies and diets. *Malacologia* 23:427-428.
- Schellema, A. H. 1985. The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca: Chaetodermomorpha). *Biological Bulletin (Woods Hole)*, 169:484-529.
- Schmidt, W. J. 1959. Bemerkungen zur Schalenstruktur von *Neopilina galathea*. *Galathea Report* 3:73-77.
- Stasek, C. R. 1972. The molluscan framework. In: *Chemical Zoology*, Vol. 7, Mollusca, M. Florin and B. T. Scheer, eds. pp. 1-44. Academic Press, New York.
- Thiele, J. 1913. Antarktische solenogastren. *Deutsche Südpolar-Expedition* 14. *Zoologie* 6:35-65.
- Trueman, E. 1976. Locomotion and the origins of Mollusca. In: *Perspectives in Experimental Biology*, Vol. 1, Zoology, P. Spencer Davies, ed. pp. 455-465. Pergamon Press, Oxford.
- Vagvolgyi, J. 1967. On the origin of molluscs, the coelom and coelomatic segmentation. *Systematic Zoology* 16:153-168.
- Waller, T. R. 1980. Scanning electron microscopy of shell and mantle in the order Arcoida (Mollusca: Bivalvia). *Smithsonian Contributions to Zoology* No. 313. 58 pp.
- Wierzejski, A. 1905. Embryologie von *Physa fontinalis*. *Zeitschrift für wissenschaftliche Zoologie* 83:502-706.
- Wilbur, K. M. and A. S. M. Saleuddin. 1983. Shell formation. In: *The Mollusca*, Vol. 7, Physiology, K. M. Wilbur and A. S. M. Saleuddin, eds. pp. 236-287. Academic Press, New York.
- Wingstrand, K. G. 1985. On the anatomy and relationships of Recent Monoplacophora. *Galathea Report* 16:1-94.



# Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei*

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**ABSTRACT:** *Prochaetoderma yongei*, an aplacophoran mollusc with a wide geographic distribution between 450 and 2200 m depth and high densities in the North American Basin, grows to adult size within 2 mo and sexual maturity within 1 yr. Gametogenesis was asynchronous within individuals from a single sled-trawl sample. Periods of increased recruitment and numbers of ripe individuals occur; whether these recurrent periods are irregular or cyclic at regular intervals is not known. Males usually outnumber females in all size classes. The peak class in length-frequency distributions contains individuals less than 1 yr old. Repopulation of a disturbed area by this species may require about a decade. The rapid growth to maturity by *P. yongei* and its ability to colonize are attributes adapted to transient or disturbed environments, but its low egg numbers and lack of synchrony in egg development are not.

## INTRODUCTION

*Prochaetoderma yongei* Scheltema has a wide geographic range, from the North American Basin in the northwestern Atlantic to the West European Basin and southward to the Namibia Basin in the eastern Atlantic. It ranges in vertical depth from 450 to about 2200 m (Scheltema 1985a, b). In the western Atlantic it occurs at densities up to  $400\text{ m}^{-2}$ , and in recent replicate samples taken over 6 seasons at 1500, 1600, and 2000 m depth off Delaware Bay (USA), it ranked 4th in numerical dominance among all stations (Maciolek et al. 1986). The congeneric species *Spathoderma clenchi* Scheltema ranked 5th, and these 2 aplacophorans formed 3.7 and 3.3 %, respectively, of the total fauna. The next most numerous mollusc was a bivalve, which ranked 25th. In the eastern Pacific another member of the family, *Chevroderma whitlatchi* Scheltema, occurs at densities of  $178\text{ m}^{-2}$  in the Panama Basin and  $124\text{ m}^{-2}$  in the Aleutian Trench; in the latter, it ranks second in abundance. The question quite naturally arises, why are these particular molluscs so successful in the deep sea?

With much of the globe covered by deep oceanic sediments, it is perhaps not too surprising to find that the burrowing, worm-shaped aplacophoran molluscs are common and well adapted to both an infaunal and epifaunal existence. However, only among the Pro-

chaetodermatidae are such high densities attained. This abundance may in part be due to their ability to feed on a wide range of sizes of organic particles (Scheltema 1981). It is the purpose of this paper to examine what part growth and reproduction may play in accounting for their abundance.

## MATERIALS AND METHODS

The Prochaetodermatidae are a deep-sea molluscan group in which it is relatively easy to examine reproduction because the single gonad lies dorsally as a discrete sac and can be readily dissected free of the digestive gland (Fig. 1; Scheltema 1985a, Fig. 2A). In addition, most specimens of *Prochaetoderma yongei* are translucent and presence or absence of the gonad and sex of mature individuals can be determined without dissection.

The numbers and lengths of males, females, and juveniles were determined for 7 samples taken at different depths in the North American Basin and in 5 summer or early fall and 2 winter months of different years using various types of gear (Table 1). Lengths of individuals were measured with dividers or a digitizer; accuracy of length measurements is discussed in Scheltema (1985a). For a summer and a winter sample taken at 2000 m by epibenthic sled (Stns 115, 210),

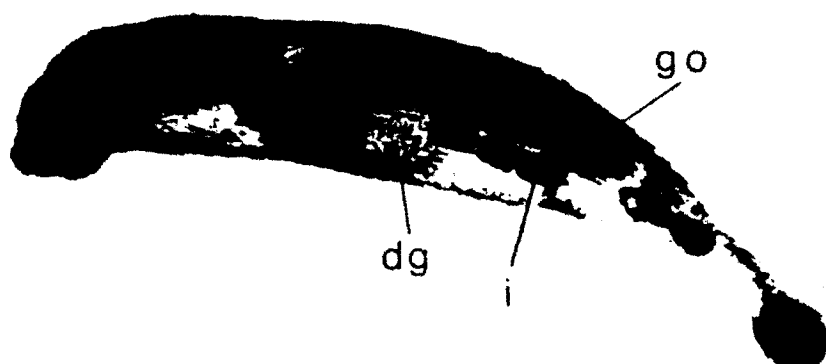


Fig. 1 *Prochaetoderma yonge*, adult male dg digestive gland, go gonad, i intestine. Length of specimen = 2.6 mm

Table 1. Samples from which lengths of males, females, and juveniles of *Prochaetoderma yonge* were measured (listed in order of month)

Station or Dive No.*	Date	Latitude (N)	Longitude (W)	Depth (m)	Gear <sup>b</sup>	Sample N
OC-10 Stn 367	Jul 76	39°45' 5"	70°37' 2"	1764	SBC #1	46
OC-10 Stn 370	Jul 76	39°44' 9"	70°35'	1815	SBC #2	20
All-12 Stn 73	Aug 64	39°46' 5"	70°43' 3"	1470	ES	133
All-24 Stn 115	Aug 66	39°39' 2"	70°24' 5"	2030	ES	100 <sup>c</sup>
AL 459, 460	Sep 72	39°46'	70°40'	1760	SC	18
All-30 Stn 128	Dec 66	39°46' 5"	70°45' 2"	1254	ES	44
CH-88 Stn 210	Feb 69	39°43'	70°46'	2024	ES	72

\* AL: DSRV *Alvin*; OC: R/V *Oceanus*; All: R/V *Atlantis II*; CH: R/V *Chin*  
<sup>b</sup> SBC: spade box core 0.25 m<sup>2</sup> (#1, 25 subcores sampled; #2, inner 9 cores only sampled); ES: epibenthic sled; SC: tube corer manipulated from submarine; ten 35 cm<sup>3</sup> cores lumped  
<sup>c</sup> All eggs measured in each female

gonads were dissected from females into a drop of glycerine and all eggs 20  $\mu$ m in diameter or greater were measured by taking the mean of the longest dimension and the length perpendicular to it. The entire winter sample (Stn 210, N = 72) was examined; a subsample of 100 individuals was randomly selected from the summer sample (Stn 115, N = 175) by swirling the entire sample into a pile and physically dividing it in two. That N = 100 exactly is coincidence; the remaining 75 individuals have the same proportion of juveniles. Stn 73 (N = 133) is likewise a subsample.

## RESULTS

Even though samples are neither replicates nor sequential, certain inferences can be made about the structure and dynamics of the populations they represent.

### Ratio of males to females

In epibenthic-sled samples, there were 1.3 to 2.0 times more males than females (Table 2). In cores, males either equaled females (sample N = 46) or were fewer than females (sample N = 20 or less). In one large box core sample, data exist for each of 25 subcores (Stn 367); a test of goodness-of-fit to Poisson distribution for males, females, and juveniles showed males to be non-randomly distributed and females and juveniles to be randomly distributed. Thus, small core samples may not capture males evenly, resulting in ratios of 1.0 or less.

In all but one sample (Stn 115) there was no significant difference between mean lengths of males and females. Sex is already fixed in immature specimens with either spermatocytes or oocytes present in gonads in very early stages of development. Thus, males and females probably grow at about the same rate. The

Table 2. *Prochaetoderma yongei*. Ratio of males to females in 7 samples

Station or Dive*	Gear*	Male		Female		Ratio M/F
		N	$\bar{X}$ length mm $\pm S_1$	N	$\bar{X}$ length mm $\pm S_1$	
367	SBC	19	1.7 $\pm$ 0.1	19	1.7 $\pm$ 0.1	1.0
370	SBC	6	2.2 $\pm$ 0.2	8	2.0 $\pm$ 0.1	0.8
73	ES	68	2.1 $\pm$ 0.1	47	2.1 $\pm$ 0.1	1.4
115	ES	44	2.2 $\pm$ 0.07	35	2.0 $\pm$ 0.05	1.3
459, 460	SC	2	1.9 $\pm$ 0.1	4	1.7 $\pm$ 0.6	0.5
128	ES	27	1.9 $\pm$ 0.1	16	1.9 $\pm$ 0.1	1.7
210	ES	45	2.0 $\pm$ 0.09	22	2.0 $\pm$ 0.5	2.0

\* See Table 1

preponderance of males is curious in the absence of obvious evidence for protandry.

#### Length distribution of males and females

Specimens were considered as male or female if spermatocytes or oocytes about 20  $\mu$ m or larger could be detected.

Males and females are distributed rather evenly by length along a normal curve, which is steeper for males when they are more numerous (Fig. 2). It is not known whether age and length are correlated beyond 2 mm; it can only be said that all size classes with individuals in which sex can be determined fall into a normal curve, with the modal class for males and females the same or within one class of each other.

The above generalizations seem to hold whether samples are taken by epibenthic sled (Fig. 2) or by quantitative gear large enough to ensure a sample number of at least 40, although in the latter instance the rarer large specimens may not occur (Fig. 3). The 2 samples reported here with 20 or fewer individuals were collected from a surface area of only 350 cm<sup>2</sup> and 900 cm<sup>2</sup> (AL 459, 460 and OC-10 Stn 370, respectively), and the length frequencies did not produce recognizable curves.

#### Proportion of juveniles

Specimens were considered to be juveniles if the gonad could not be detected or appeared as a thin line.

The percentage of juveniles ranged from 2.3 to 66.7 %, with lowest values occurring in the 2 winter samples and the highest in the 5 summer and early fall samples (Table 3). A comparison of distributions by length of juveniles, males, and females in a summer and a winter sled trawl sample from 2000 m shows a bimodal distribution in the summer sample that is not present in the winter sample (Fig. 2). The 2 samples

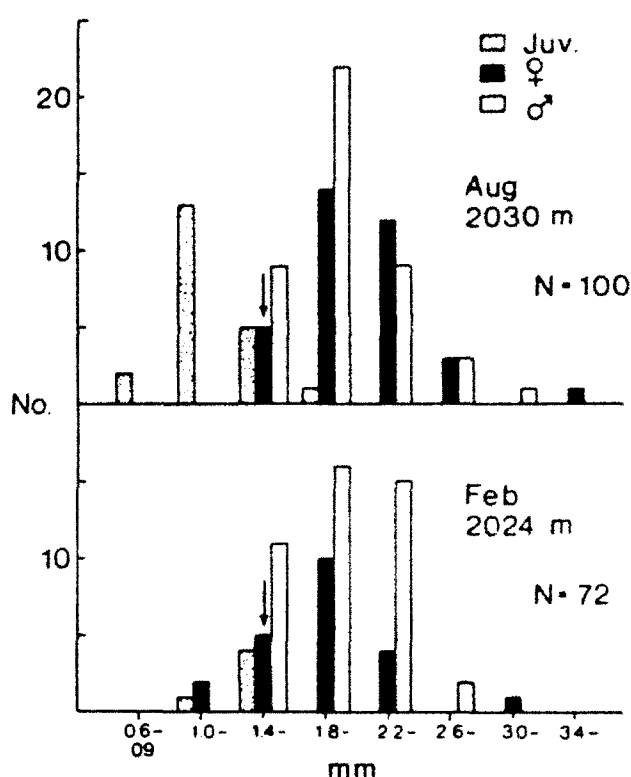


Fig. 2. *Prochaetoderma yongei*. Length-frequency distributions of juveniles, females, and males in two 2000 m samples from approximately the same location taken with an epibenthic sled trawl in Aug and 2½ yr later in Feb. Arrows over bars for females denote smallest size class with mature eggs. (Aug sample: Stn 115, Feb sample: Stn 210; see Table 1)

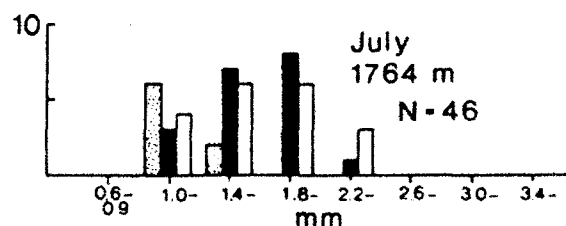


Fig. 3. *Prochaetoderma yongei*. Length-frequency distributions of juveniles, females, and males in a 0.25 m<sup>2</sup> spade box core taken at 1764 m in Jul (Stn 367; see Table 1). Bar conventions as in Fig. 2

Table 3. *Prochaetoderma yongei*. Percentage of juveniles ranked by month

Month/ year	Stn/ Dive*	Gear*	Depth	Total sample (N)	% Ju- veniles
Jul 76	367	SBC	1764	46	17.4
Jul 76	370	SBC	1815	20	30.0
Aug 64	73	ES	1470	133	13.5
Aug 66	115	ES	2030	100	21.0
Sep 72	459, 460	SC	1760	18	66.7
Dec 66	128	ES	1254	44	2.3
Feb 69	210	ES	2024	72	6.9

\* See Table 1

were taken 2½ yr apart. Another winter sample examined, also a sled trawl but from about 1200 m (Stn 128, Table 1), had only a single juvenile, while a summer trawl sample from about 1400 m (Stn 73) had the same bimodal frequency-distribution for juveniles and males/females as the August 2000 m station. This bimodality in length-frequency is seen only if juveniles are plotted separately from the adults; owing to their rapid growth, juveniles overlap mature adults in length (see below). A single curve will result if juvenile and adult length frequencies are combined. The graphs of summer and winter size distributions show that recruitment does not occur at a constant rate, but the samples are too few to be certain that the differences reflect seasonal periodicity.

The clear bimodality of summer populations collected from 1400 and 2000 m by epibenthic sled appears dampened in a large box-core summer sample from 1764 m (Fig. 3). In this sample there is a larger proportion of small males and females than in the epibenthic-sled summer samples, a situation which may reflect either a difference in mean lengths among the populations, a patchy distribution in age classes, or collecting bias by the different types of gear.

The high percentage (66.7 %) of juveniles in 10 tube cores (350 cm<sup>2</sup> total area) collected by submarine in September 1972 at 1760 m (Table 3) was not duplicated in 0.25 m box-core samples from the same locality 4 yr later in July 1976 or in a 169 cm<sup>2</sup> core taken by submarine in September 1978 which contained no juveniles at all. These differences in proportions of juveniles in core samples may be due to irregular, non-cyclic recruitment into the population or to patchy settlement of juveniles at a spatial scale such that their presence was not detected.

#### Egg development and production

The total number of eggs larger than 20 µm in diameter ranges from 4 to 6 in immature individuals up

to 39 in mature females; the average number per female was 21 in the August trawl sample (Stn 115) and 14 in the February trawl sample (Stn 210). Various stages of development and egg sizes are present in all individuals. Three egg stages were determined as follows (Fig. 4). Stage I eggs have 2 or several nucleoli, a distinct nuclear membrane, and semi-translucent yolk granules; diameters range from 20 to 96 µm. Stage II eggs have a single large nucleolus greater than 12 µm in diameter, a distinct nuclear membrane, and dense yolk granules; diameters range from 55 to 177 µm. Eggs are considered to be mature (Stage III) when the nuclear membrane disappears and the nucleolus is less than 10 µm or absent; diameters range from 90 to 226 µm. Mature eggs are free in the lumen of the gonad; there is a distinct clear area between the vitelline membrane and yolk. (The great range in size of so-called 'mature' eggs may reflect an inadequacy in definition.) The distinction among stages was unambiguous; the implication is that development from one stage to the next is rapid.

In general, Stage I eggs are less than 60 µm; most eggs from 100 to 120 µm are Stage II eggs; and 'mature' eggs are usually greater than 140 µm. Eggs about to be spawned elongate as they move down the narrow gonopericardial duct and account for egg measurements 190 µm and larger (Fig. 4D).

The size frequency of mean diameters for each stage was plotted for each female from the August and February sled trawls from 2000 m (Fig. 5). The larger size and number of Stage III eggs in the August sample than in the February sample perhaps indicate a potentially higher spawning rate; they co-occur with the greater number of small juveniles in the August sample. The percentage of females with mature eggs in August was 82 %, more than 1½ times the percentage (48 %) in February (Table 4). All 3 oocyte stages are present in 77 % of the August females, but only 33 % of February females have all stages. The mean of means of egg diameters for all females and number of eggs per female for each stage also indicate greater potential reproductive activity in the August population than in the February population (Table 4); however, there is no significant difference in size of Stage I and II eggs in the 2 samples.

#### Data on growth and reproduction from experimental boxes

Two sets of data are available for *Prochaetoderma yongei* from experimental boxes of azoic mud placed by submarine at 1760 m (Table 5); 2 more sets of data are available from free-vehicle boxes of azoic mud deployed at 2020 m, the same depth but not location as



Fig. 4. *Prochaetoderma yongei*. Egg developmental stages. (A) Stage I with transparent yolk, nuclear membrane, and 2 large, or one large and several small, nucleoli. (B) Stage II with dense yolk granules, large nucleolus and nuclear membrane. (C) Stage III, a mature egg with no nuclear membrane or nucleolus. (D) Mature egg within gonopericardial duct. n: nucleolus; N: nuclear membrane; g: wall of gonopericardial duct; i: intestine. Scale = 100  $\mu$ m

the August and February trawl samples described above (Stn 115, 210). From recruitment of *P. yongei* into these experimental boxes, estimates can be made of the minimum growth rate and maximum time to reach reproductive maturity.

Recruitment into experimental boxes is considered to be by larvae. Although the embryology is not known for any chaetodermomorph, there is no indication for direct development or brooding in Prochaetodermatidae. In the other group of aplacophorans, the footed Neomeniomorpha, 3 species are known to

release zygotes and have free-swimming larvae; egg sizes range from 120 to 260  $\mu$ m (Hadfield 1979, Table 2). Mean mature egg sizes of *Prochaetoderma yongei* from February and August samples are 141 and 165  $\mu$ m, respectively (Table 4), and fall within the sizes expected for aplacophorans with larvae.

Because *Prochaetoderma yongei* burrows, it is not likely that it has crept up the sides of an experimental box, nor can recruitment have occurred by lateral transport. The most likely explanation for the existence of *P. yongei* in experimental boxes is by larval settle-

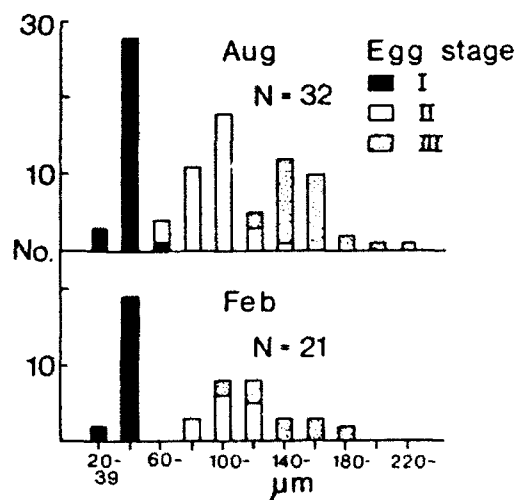


Fig. 5. *Prochaetoderma yongei*. Frequency distribution of egg developmental stages in females from the 2000 m Aug and Feb samples shown in Fig. 2. Mean diameter is plotted for each stage in each female. Discrepancies in numbers of females (N) between this figure and Table 2 reflect incomplete gonad dissections

ment, and growth is assumed to have taken place there.

The following data, which are pertinent in interpreting results from experimental boxes, are from all specimens of *Prochaetoderma yongei* listed in Table 1:

Largest egg measured	diameter 226 µm
Smallest juvenile measured	length 0.3 mm
Largest juvenile measured	length 1.8 mm
Smallest female with mature eggs	length 1.7 mm
Smallest specimen determined to be male	length 1.0 mm
Smallest specimen determined to be female	length 1.3 mm

A juvenile specimen of *Prochaetoderma yongei* measuring 1.4 mm in length was recovered from a 2 mo box (Table 5, *Alvin* 597). This is the size at which

developing gonads have first been seen; it is nearly 5 times larger than the smallest recorded juvenile.

A single male occurred in a 6 mo box from 2020 m (MID-6, Stn 2). It was 2.6 mm in length, longer than the mean lengths recorded for males from the 2000 m epibenthic-sled samples (Stn 115, 2.2 mm; Stn 210, 2.0 mm; Table 2) and longer than the largest known juvenile (1.8 mm).

Ten specimens were recovered from three 8 mo boxes: 2 juveniles, 5 males, and 3 females (*Alvin* 834). Two of the females were less than 1.7 mm, the size individual in which mature eggs have first been seen. The largest female (2.1 mm), although large enough to be sexually mature, had only immature eggs smaller than 75 µm. Lengths of males varied between 1.7 and 2.3 mm, from less than the largest juvenile to greater than the average for any of the stations (Table 2). Like most other populations sampled by trawl or cores, there were more males than females (1.7 times).

A female 2.1 mm in length was found in a 12 mo box at 2020 m recovered in May (MID-4 Stn 2). This individual had 4 Stage III ('mature') eggs having a mean diameter of 152 µm; egg number totaled 15. Table 6 compares this specimen with females from an August 2000 m trawl sample for which eggs were measured (Stn 115, Tables 1 & 4). There is no significant difference between the female from the experimental box and the summer trawl sample females in length or in mean diameters of egg Stages I, II, and III; thus this individual is considered to be mature.

Recruits into the experimental boxes indicate that both growth and development to maturity are rapid in *Prochaetoderma yongei*, as fast as or faster than many common subtidal molluscs of the temperate zone. A recruit can grow within 2 mo to a minimum size at

Table 4. *Prochaetoderma yongei*. Egg number per female and egg diameter mean of means for developmental Stage I, II, and III in Feb 1969 and Aug 1966

Stage	Mean no. eggs female <sup>-1</sup> (range)	Feb <sup>a</sup> $\bar{X}^c$ egg diameter (µm)	S <sup>2</sup>	% females with eggs	Mean no. eggs female <sup>-1</sup> (range)	Aug <sup>b</sup> $\bar{X}^c$ egg diameter (µm)	S <sup>2</sup>	% females with eggs	t-test $\bar{X}$
I	11.6 (4-25)	46	28.29	100.0	12.7 (5-29)	47	28.393	100.0	ns
II	1.6 (0-4)	114	456.84	71.4	4.3 (0-11)	106	272.94	97.0	ns
III	0.6 (0-2)	141	504.93	47.6	2.6 (0-13)	165	443.31	81.8	p < 0.01

<sup>a</sup> 39° 43.0'N, 70° 46.0'W, 2024 m; CH-88 Stn 210

<sup>b</sup> 39° 39.2'N, 70° 24.5'W, 2030 m; AII-24 Stn 115

<sup>c</sup>  $\bar{X} = \frac{\sum X}{N}$  where  $\bar{X}$  is mean egg diameter for each female and N is total number of females. Individuals without Stage II and III eggs are not included in the computation for that stage

Table 5. *Prochaetoderma yongei*. Colonization data for specimens from experimental boxes

Station	Date recovered	Total mo (d) of experiment	Juvenile	Length mm Male	Female	Largest egg diameter (μm)
<b>1760 m; 39° 46' N, 70° 40' W</b>						
Alvin Dive 597	30 Aug 75	2 (60)	1.4	0	0	—
Alvin Dive 834	18 Sep 78	8 (248)				
Box A			0	1.7	1.4	< 75
(with screen cover)				1.7	1.4	75
Box C			1.7	1.7	2.1	< 75
(with screen cover)				2.3		
Box D				2.0		
(without screen cover)			1.0	0	0	—
<b>2020 m; 38° 35.78' N, 72° 53.65' W</b>						
*MID-4 Stn 2						
Free Vehicle C	20 May 85	12 (359)	0	0	2.1	162
Tray 2						
*MID-6 Stn 2						
Free Vehicle H	12 Dec 85	6 (179)	0	2.6	0	—
Tray 6						
* See Maciolek et al. (1986)						

\*See Maciolek et al. (1986)

Table 6. *Prochaetoderma yongei*. Comparison of a female from a 1 yr experimental box with females from an Aug trawl sample at 2000 m: body length; and egg number per female and mean egg diameter by developmental stage

	Aug trawl sample <sup>a</sup>	1 yr exp. box <sup>b</sup>	t-test
Total N females	35	1	
Mean length mm $\pm$ SD	2.2 $\pm$ 0.07	2.1	ns
Stage I eggs: $\bar{X}$ diam. ( $\mu$ m) $\pm$ $S_{\bar{x}}$	47 $\pm$ 0.8 <sup>c</sup>	44	ns
No. female <sup>-1</sup>	12.0	10	
Stage II eggs: $\bar{X}$ diam. ( $\mu$ m) $\pm$ $S_{\bar{x}}$	106 $\pm$ 3.0 <sup>c</sup>	101	ns
No. female <sup>-1</sup>	3.9	1	
Stage III eggs: $\bar{X}$ diam. ( $\mu$ m) $\pm$ $S_{\bar{x}}$	165 $\pm$ 4.1 <sup>c</sup>	152	ns
No. female <sup>-1</sup>	2.3	4	

<sup>a</sup> 39°39.2'N, 70°24.5'W, 2030 m; All 24 Stn 115<sup>b</sup> 38°35.78'N, 72°53.65'W, 2020 m; MID-4 Stn 2<sup>c</sup>  $\bar{X} = \frac{\sum X}{N}$ . See Table 4 for variances and footnote

which gonad maturation may proceed and reach sexual maturity within a year. These are maximum estimates, since the actual time of recruitment into the boxes is unknown. It may be only fortuitous that in the 8 mo experiments, development of female specimens fell between the 2 and 12 mo experiments.

#### Correlation of growth data from experimental boxes and length-frequency histograms

When length frequencies of juveniles are separated from those for males and females, the pulse of recruitment which occurred in summer samples has a peak size class of 1.0 to 1.3 mm (Fig. 2 & 3). Recruits into experimental boxes show that a length of 1.4 mm can

be attained within 2 mo, and 2 mm or greater within 6 mo (Table 5). Therefore, evidence from length frequencies for a pulse in recruitment would probably disappear after 2 mo.

Sexual maturity is experimentally known to be reached within 1 yr (Tables 5 & 6). As there are mature females in the 1.4 to 1.7 mm size class (Fig. 2), it can be assumed that that size class contains individuals whose ages span 2 mo to 1 yr. The peak size class in both summer and winter samples of Fig. 2 & 3 is 1.8 to 2.1 mm; included in this class are individuals of 6 mo in age or less, since the recruit into a 6 mo experimental box was 2.6 mm (Table 5). Thus growth during 1 yr is included in size classes from 0.6 to 2.6 mm and falls within the peak size class.

The age beyond 1 yr or mortality at any age cannot be inferred from the growth and recruitment data given here.

#### Data on recruitment rate from experimental boxes

The faunal contents of the 8 mo experimental boxes are directly comparable to box core samples taken from the same locality (Stn 367) or slightly deeper (Stn 370). All are 0.25 m<sup>2</sup> in area with twenty-five 10 cm<sup>2</sup> subsections; all can be considered summer populations, albeit the termination of the experimental box was 1 yr after the box cores were taken. The numbers of *Prochaetoderma yongei* per 10 cm<sup>2</sup> subcore in the 2 box cores were 1.8 and 2.2 (Stn 367 and 370, respectively), or an average of 2.0. In each screened experimental box (Alvin 834A and C, Table 5) the number of *P. yongei* per 10 cm<sup>2</sup> subsection was 0.2 specimens. Thus, if it takes 248 d to recruit 0.2 individuals per 10 cm<sup>2</sup>, then it would take 2480 d or about 7 yr to recruit to numbers found in the natural population, all else being equal and ignoring predation, variation in rates of recruitment, and recruitment by lateral transport (but see Smith [1985] on the importance of disturbance and lateral transport). Predation may account for the absence of *P. yongei* in a 26 mo unscreened experimental box placed in the same area several years earlier (Grassle 1977) and the presence of only a single individual in the 8 mo unscreened experimental box (Table 5, Alvin 834D).

### DISCUSSION

Reproduction of invertebrates in level bottom communities of the deep sea should reflect the effects of a stable environment of permanent darkness, low temperatures, and great pressure. Thus the questions of whether there is reproductive periodicity in such an environment and what the growth rates might be are of interest.

Certain terms are used in the following discussion of reproductive patterns. They are defined as follows: 'asynchrony' and 'synchrony' refer to both gametogenesis and spawning. Gametogenesis is considered asynchronous if several stages of oocyte development are present in each female in a population; it is assumed, but cannot be observed, that at least some females are spawning at any one time (period undefined) and that the population as a whole never stops reproducing. Gametogenesis is synchronous when all oocytes in all females are at the same stage in a population; synchronous spawning, or the release of

all eggs, can be seen to have occurred by examination of the gonads. 'Recruitment' includes such considerations as type of development, presence or absence of a dispersal stage, conditions affecting settlement, and mortality of early postlarvae; here recruitment refers only to the presence of juveniles in a population as indicated by size frequencies of individuals. Three terms define time as it relates to reproductive events. 'Continuous' reproduction has a steady rate of mature oocyte production and recruitment into a population; it can only result from asynchrony of gametogenesis. 'Periodic' reproduction has regularly reoccurring cyclic gametogenesis and spawning that can only result from synchrony. Continuous reproduction overlaid by periods of increased intensity of reproduction is here called 'fluctuating'; it also results from asynchrony and may be either cyclic or irregular in occurrence. 'Fecundity', the total reproductive capacity of an individual over its lifetime, is not treated here.

The earliest measurements of reproduction in deep-sea level-bottom molluscs were based on histologic examination of gamete development and gonad volume in the bivalve genus *Nucula* (Scheltema 1972; preliminary findings quoted in Sanders & Hessler 1969). In at least one species some portion of a population had mature eggs year-round. Scheltema suggested that 'deep-sea species must either survive better, live longer, or reproduce more continuously than their counterparts on the shelf' in order to maintain a fecundity equal to sublittoral species but that little was known about periodicity of reproduction in the deep sea.

Later studies have addressed both recruitment and gametogenesis by comparing gamete development, oocyte size-frequencies, and length frequencies among individuals from single populations over time. These studies show that among species of deep-sea molluscs 3 patterns of reproduction can be discerned: continuous-asynchronous, periodic-synchronous, and fluctuating-asynchronous. In continuous-asynchronous reproduction no cyclic events are observed, juveniles are always present in the same proportion in a population, and some or all females have ripe eggs at all times (e.g. gastropods: *Benthonella tenella*, Rex et al. 1979 [although size-frequencies were erratic]; *Colus jeffreysianus*, Colman et al. 1986; bivalves: *Nucula darella*, *Tindaria cervola*, Rokop 1974, 1979). Periodic-synchronous reproduction results in cyclic spawn-out over an entire population followed by peaks in recruitment (e.g. bivalves: *Ledella messanensis* and *Yoldiella jeffreysi*, where the cycle is seasonal, Lightfoot et al. 1979, Gage 1985). Fluctuating-asynchronous reproduction occurs in species which have the capacity for continuous reproduction but which nevertheless have times of increased recruitment and production of



mature oocytes (e.g. bivalves: *Nucula cancellata*, Gage et al. 1986).

The rate of recruitment can vary within a pattern of reproduction. For instance, among certain deep-sea bivalves that reproduce continuously more than 25 % of all individuals within a population may be juveniles (Rokop 1979), whereas in the gastropod *Colus jeffreysianus*, also a continuously reproducing species, only a few juveniles occur in a population at one time (Colman et al. 1986).

Among the 3 patterns, *Prochaetoderma yongei* has a fluctuating-asynchronous reproduction. Females have more than one stage of oocyte development, a population has some ripe individuals at all times, and there are fluctuations in number of ripe individuals, size and proportion of mature oocytes, and proportion of juveniles. It is not certain from data presented here that the fluctuations are seasonal.

The time needed for juveniles to reach sexual maturity has been estimated in a few instances from length-frequency data and expressed in qualitative terms, e.g. Rokop (1979) described the rapid advent of sexual maturity in some bivalves. Graphs of length-frequency data from the deep sea have so far not been related to known time intervals, but age structure underlying length frequencies in 4 bivalve species collected over many seasons and years in the Rockall Trough has been modeled by Gage et al. (1986) after estimating age from shell growth-lines; maturity is apparently achieved in 2 to 3 yr. Turekian et al. (1975) estimated from radiometric measurement that the shell of an abyssal bivalve, *Tindaria callistiformis*, was  $98 \pm 76$  yr old; by extrapolating from growth rates of shallow water species they further estimated that this specimen had reached maturity in 50 to 60 yr.

Direct measurements of time to maturation classically have depended on the ability to sample a cohort from recruitment through time, but in deep-sea populations there are difficulties in doing this: (1) the labor involved in sequential sampling (including ship time and sorting) is prohibitively expensive, and (2) the pattern of continuous and asynchronous reproduction in many deep-sea species makes time of recruitment, or release of a specific cohort, virtually unknowable. However, recruitment of juveniles and unambiguous maximum growth rates to maturity can be determined from colonization experiments for species with planktonic larval stages (see Grassle [1980] for a description of experiments). Besides the rates given here for *Prochaetoderma yongei*, 2 other experiments have yielded rapid growth rates for deep-sea molluscs; both are from about the same 1800 m area as the 2 and 8 mo experiments described above (Table 5). Mature-sized specimens of the bivalve *Nucula cancellata* were recovered from a 26 mo experimental box of azoic mud

(Grassle 1977, 1978). Wood panels exposed for 3½ mo on the sea bottom were twice colonized by each of 2 species of wood-boring bivalves (Xylophaginae) (Turner 1973). Gonads were nearly ripe in the older individuals, although the specimens were small owing to crowding. Although most published results of recruitment experiments have addressed questions of faunal recolonization rates rather than growth rates of individual species (Grassle 1977, Desbruyères et al. 1980), one of Grassle's stated purposes (1978) for recruitment experiments is to establish growth rates, and the data presented here are based on his experimental boxes.

The question of precisely how growth and reproduction traits of *Prochaetoderma yongei* affect its numerical abundance in the North American Basin remains unanswered. The ability of *P. yongei* to recruit and grow quickly to maturity, combined with its small size, is characteristic of species adapted to transient environments (so-called opportunistic species). However, lack of synchrony in reproduction and low numbers of eggs are not the marks of a species adapted to rapid change and may be contrasted to the 30 000 eggs present in individuals of the deep-sea Xylophaginae (Turner 1973). Moreover, the numerical success of *P. yongei* in the northwestern Atlantic for some reason does not continue over the rest of its range in the eastern Atlantic, where the diversity of species among the Prochaetodernatidae is very much higher but densities of individuals in a species are much lower (Scheltema 1985a, b).

The stimuli that bring about times of increased reproduction – cyclic or fluctuating – in deep-sea species remain to be ascertained and the seeming constancy of the deep sea questioned. The data presented here and from earlier studies on molluscs indicate that growth and maturation times in many deep-sea species are on the same time scale as in shallow-water species. Certainly in these cases constant low temperatures, darkness, and high pressures have not resulted in slow growth.

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## LITERATURE CITED

- Colman, J. G., Tyler, P. A., Gage, J. D. (1986). The reproductive biology of *Colus jeffreysianus* (Gastropoda: Prosobranchia) from 2200 m in the N.E. Atlantic. *J. mollusc. Stud.* 52: 45-54
- Desbruyères, D., Bervas, J. Y., Khripounoff, A. (1980). Un cas de colonisation rapide d'un sédiment profond. *Oceanologica Acta* 3: 285-291
- Gage, J. D. (1985). The analysis of population dynamics in deep-sea benthos. In: Gibbs, P. E. (ed.) *Proceedings of the Nineteenth European Marine Biology Symposium*. Cambridge University Press, Cambridge, p. 201-212
- Gage, J. D., Tyler, P. A., Davies, G., Harvey, R. (1986). Life-history studies on deep-sea prosobranch bivalves from the Rockall Trough (NE Atlantic). Heppell, D. (ed.) *Ninth International Malacological Congress*, Edinburgh, Scotland, 31 Aug- 6 Sep (Abstract). National Museums of Scotland, Edinburgh, p. 27
- Grassle, J. F. (1977). Slow recolonisation of deep-sea sediment. *Nature*, Lond. 265: 618-619
- Grassle, J. F. (1978). Diversity and population dynamics of benthic organisms. *Oceanus* 21 (1): 42-49
- Grassle, J. F. (1980). *In situ* studies of deep-sea communities. In: Diemer, F. P., Vernberg, F. J., Mirkes, D. Z. (ed.) *Advanced concepts in ocean measurements for marine biology*. Belle W. Baruch Lib. Mar. Sci., No. 10, Univ. of South Carolina Press, Columbia, p. 321-332
- Hadfield, M. G. (1979). Aplacophora. In: Giese, A. C., Pearse, J. S. (ed.) *Reproduction of marine invertebrates*, Vol. 5, Molluscs: Pelecypods and lesser classes. Academic Press, New York, p. 1-25
- Lightfoot, R. H., Tyler, P. A., Gage, J. D. (1979). Seasonal reproduction in deep-sea bivalves and brittlestars. *Deep Sea Res.* 26A: 967-973
- Maciolek, N., Grassle, J. F., Hecker, B., Boehm, P. D., Brown, B., Dade, B., Steinauer, W. G., Baptiste, E., Ruff, R. E., Petrecca, R. (1986). Study of biological processes on the U.S. Mid-Atlantic Slope and Rise. OCS Study MMS 86-0000, Final Draft Rept., U.S. Dept. Interior, Minerals Management Service, Washington, D. C.
- Rex, M. A., Van Ummersen, C. A., Turner, R. D. (1979). Reproductive pattern in the abyssal snail *Benthonella tenella* (Jeffreys). In: Stancyk, S. E. (ed.) *Reproductive ecology of marine invertebrates*. Belle W. Baruch Lib. Mar. Sci., No. 9, Univ. of South Carolina Press, Columbia, p. 173-188
- Rokop, F. J. (1974). Reproductive patterns in the deep-sea benthos. *Science* 186: 743-745
- Rokop, F. J. (1979). Year-round reproduction in the deep-sea bivalve molluscs. In: Stancyk, S. E. (ed.) *Reproductive ecology in marine invertebrates*. Belle W. Baruch Lib. Mar. Sci., No. 9, Univ. of South Carolina Press, Columbia, p. 189-198
- Sanders, H. L., Hessler, R. R. (1969). *Ecology of the deep-sea benthos*. *Science* 163: 1419-1424
- Scheltema, A. H. (1981). Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia* 20: 361-383
- Scheltema, A. H. (1985a). The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma* n.g. and *Spathoderma* n.g. (Mollusca: Chaetodermomorpha). *Biol. Bull. mar. biol. Lab., Woods Hole* 169: 484-529
- Scheltema, A. H. (1985b). The genus *Prochaetoderma* (Aplacophora, Mollusca): initial account. In: Laubier, L., Monniot, C. (ed.) *Peuplements profonds du Golfe de Gascogne*. IFREMER, Brest, p. 391-396
- Scheltema, R. S. (1972). Reproduction and dispersal of bottom dwelling deep-sea invertebrates: a speculative summary. In: Bauer, R. W. (ed.) *Barobiology and the experimental biology of the deep sea*. School of Public Health, Univ. of North Carolina, Chapel Hill, p. 58-68
- Smith, C. R. (1985). Colonization studies in the deep sea: are results biased by experimental designs? In: Gibbs, P. E. (ed.) *Proceedings of the Nineteenth European Marine Biology Symposium*. Cambridge University Press, Cambridge, p. 183-189
- Turekian, K. K., Cochran, J. K., Kharkar, D. P., Cerrato, R. M., Vaisnys, J. R., Sanders, H. L., Grassle, J. F., Allen, J. A. (1975). Slow growth rate of a deep-sea clam determined by  $^{226}\text{Ra}$  chronology. *Science* 72: 2829-2832
- Turner, R. D. (1973). Wood-boring bivalves, opportunistic species in the deep sea. *Science* 180: 1377-1379

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THE APLACOPHORAN FAMILY PROCHAETODERMATIDAE IN THE  
NORTH AMERICAN BASIN, INCLUDING *CHEVRODERMA* N.G. AND  
*SPATHODERMA* N.G. (MOLLUSCA; CHAETODERMOMORPHA)\*

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ABSTRACT

Six species in three genera of Prochaetodermatidae are described from over 650 stations and 5200 specimens in the Atlantic and north Pacific Oceans from depths between 500 and 7300 m. Included are all species in the North American Basin and all species in *Chevroderma* n.g.

Three principal characters differentiate prochaetodermatid species and genera: spicules, radula, and body shape. Family membership is defined by radula and jaws, spicule morphology determines genus, and species are described by spicules and radula. Mean body shape describes populations of species. Interference colors produced by the aragonite spicules indicate spicule thickness and symmetry. The variation in *Prochaetoderma yongei* n. sp., described in detail, establishes the taxonomic base on which to judge the morphological limits of a prochaetodermatid species.

*Spathoderma* n.g. and *Chevroderma* n.g. differ from each other and from the genus *Prochaetoderma* in spicule morphology. *P. yongei* and *S. clenchi* n. sp. are widespread northwestern and eastern Atlantic continental slope and abyssal rise species. *C. turnerae* and *C. gauson* n. spp. are abyssal species, the former occurring throughout the Atlantic, the latter only in the northern West European Basin. *C. scalpellum* n. sp. is a slope species of restricted range in the eastern Atlantic. *C. whittlatchi* n. sp. is a wide-ranging abyssal and hadal species of the northern east and mid-Pacific. A wide geographic range is correlated with a vertical depth distribution greater than 1500 m.

All species are patchy in distribution but particular species can be numerically dominant and occur at high densities locally, e.g., up to 400 m<sup>-2</sup> for *P. yongei* and 178 m<sup>-2</sup> for *C. whittlatchi*. In the north Atlantic, greatest numerical abundances and lowest diversity of Prochaetodermatidae occur in the North American Basin.

INTRODUCTION

Aplacophoran mollusks belonging to the family Prochaetodermatidae are the most numerous and widespread of the Chaetodermomorpha in the deep sea. They have been taken at all depths in the north and south Atlantic Ocean, Mediterranean Sea, central, north and east Pacific Ocean, and in the western Pacific off southeastern Australia (unpub. data). Particular species are sometimes numerically among the most abundant macrofaunal species in quantitative samples and are thus an important part of the deep-sea fauna (Scheltema, 1981).

Previously the family has consisted of only two named species belonging to the genus *Prochaetoderma*: *P. raduliferum* (Kowalevsky 1901) from the Mediterranean and *P. californicum* Schwabl 1963 from the troughs off southern California, although other unnamed species have been figured (Treece, 1979, Fig. 5; Scheltema, 1978, Figs.

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1A, 2, 3B; 1981, Figs. 1D, 2E-G, 3D-H, K, 7, 11A-C). Collections taken in the last two decades from both the Atlantic and Pacific Ocean contain several new species and genera belonging to this family.

Six new species in three genera are described here, including all the species that occur in the North American Basin and all those so far collected that belong to the new genus *Chevroderma*. The variation in one species, which has a broad geographic range, is described in detail to establish the taxonomic base on which to judge the morphological limits of a species in the family Prochaetodermatidae.

#### MATERIALS AND METHODS

Descriptions are based on examination of more than 5200 specimens from the Atlantic Ocean and 68 from the Pacific including the following regions (Tables I, II; Fig. 1): in the Atlantic west of the Mid-Atlantic Ridge—North American Basin, Newfoundland Basin, Brazil Basin, and Argentine Basin; in the Atlantic east of the Mid-Atlantic Ridge—West European Basin, Canary Basin, Cape Verde Basin, Angola Basin, and Namibia Basin; in the eastern Pacific—Panama Basin, Galapagos vents area, off southern California, off Oregon, and Aleutian Trench; and in the mid-Pacific—just north of the Equator.

Samples were taken with a variety of quantitative and nonquantitative gear. The latter included several types of trawls and epibenthic sleds, and the former, box and tube corers manipulated from submersibles and box corers and anchor dredges put overboard (see footnote, Table I).

Most samples were screened using a flotation method (Sanders *et al.*, 1965), fixed in formaldehyde, and preserved in 70–80% alcohol on shipboard. Samples were later sorted into taxa in the laboratory.

Measurements of specimens were made by using dividers or a digitizer on lines drawn length- and crosswise on camera-lucida images at 12× or 25×. Measurements were made to the nearest 0.01 mm in the first two species described, with an accuracy of 0.05 mm; however, it was found that the precision of measurements is not greater than 0.1 mm, and all subsequent measurements are so given.

Treatment of spicules for both light transmission and scanning electron microscopy and of radulae has been previously described (A. Scheltema, 1972, 1976). Permanent preparations of spicules and radulae were made by drying them directly on a slide and mounting with a standard histological plastic medium. Spicules were also examined under cross-polarized light to measure thickness. X-ray diffraction showed them to be formed of aragonite with the long axes of the crystals parallel to the long axis of the spicule, and by comparing the highest interference color with a standard crystallographer's chart, greatest thickness was estimated to the nearest 0.5  $\mu\text{m}$ . Selected isochromes were drawn to show the pattern of thickening and symmetry of the spicules (see Fig. 2C). Length and width of spicules were measured with an ocular micrometer.

Length and width of radula teeth, central plates, and jaws (shown in Fig. 15) were measured with an ocular micrometer.

#### TYPE MATERIAL

Types are deposited in the National Museum of Natural History, Washington, DC (USNM) and the Muséum National d'Histoire Naturelle, Paris (MNHN). Each holotype is preserved in buffered 80% alcohol after removing a few spicules to a permanent slide. Specimens from the type locality and those used for illustrating spicules

TABLE I

Specimens examined, Atlantic Ocean (Prochaetoderma yongei, Spathoderma clenchi, Chevroderma turnerae, C. gausson, and C. scalpellum)

Cruise or dive no.	Station	Gear	Date	Depth m	Latitude	Longitude	P yongei	S clenchi	C turnerae	C gausson	C scalpellum
North American Basin											
					North	West					
ATLANTIS 263 or 264	E #3	AD	25/V/61	823	39°50' S	70°35'	5				
	F #1	AD	24/V/61	1500	39°47'	70°45'	7				
	G #1	AD	24/V/63	2000	39°42'	70°39'	3	1			
	H #2	AD	24/V/61	3752	38°05'	69°36'			1		
ATLANTIS 298	58	AD	7/IX/63	2000	38°34' S	72°55' W	3	1			
ATLANTIS II-12	61	AD	20/VIII/64	2000	39°43' S	70°37' E	5	2			
	62	ES	21/VIII/64	2496	39°26'	70°33'		5			
	70	ES	23/VIII/64	4680	36°23'	67°58'			6		
	73***	ES	25/VIII/64	1470	39°46' S	70°41' S	911***	19			
CHAIN-50	81	ES	2/VII/65	5042	39°41'	66°28'	71				
	84	ES	4/VIII/65	4749	36°24' S	67°56'			15		
	85	ES	5/VII/65	3834	37°59' S	69°26' E			6		
	87	ES	6/VII/65	1102	39°48' S	70°40' E	986				
ATLANTIS II-17	92	ES	13/XII/65	4694	36°20'	67°56'			3		
	95	ES	17/XII/65	3753	38°33'	68°32'			4		
CHAIN-58	103	ES	4/V/66	2022	39°43' S	70°37' S	7	18			
	104	AD	4/V/66	2050	39°41' S	70°35' S		1			
	105	ES	5/V/66	530	39°56' S	71°03' S					
ATLANTIS II-24	115	ES	16/VIII/66	2030	39°39' S	70°24' S	1				
	120	ES	20/VIII/66	5018	34°43' S	66°32' E	175	211			
	121	ES	21/VIII/66	4800	35°50' S	65°11' S			2		
	122***	ES	21/VIII/66	4833	35°50' S	64°57' S			6		
	125	ES	23/VIII/66	4825	37°24' S	65°54' S			12***		
	126	ES	24/VIII/66	3806	39°37' S	66°47' S			4		
ATLANTIS II-30	128	ES	16/XII/66	1254	39°46' S	70°45' S	45				
ATLANTIS II-40	131***	ES	18/XII/66	2178	39°38' S	70°36' S	21	71***	71		
	175	ES	29/XI/67	4667	36°36'	68°29'			13		
	178	AD	1/XII/67	1839	39°44' S	70°12' S	3	5			
CHAIN-88	207	ES	21/II/69	805	39°51' S	70°54' S	166				

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TABLE I (Continued)

Cruise or dive no.	Station	Gear <sup>a</sup>	Date	Depth m	Latitude	Longitude	P jonger	S clenchi	C turnerae	C gausson	C scalperium
<b>Argentine Basin</b>											
					South	West					
ATLANTIS II-60	242	ES	13/III/71	4382	38°16.9'	51°56.1'			5		
	243	ES	14/III/71	3815	37°36.8'	52°23.6'			1		
	245	ES	14/III/71	2707	36°55.7'	53°01.4'			74		
	246	ES	15/III/71	3343	37°15.1'	52°45.0'			2		
	247	ES	17/III/71	5208	43°33.0'	48°58.1'			4		
	259	ES	26/III/71	3303	37°13.3'	52°45.0'			13		
	262	ES	27/III/71	2440	36°05.2'	52°17.9'			13		
<b>West European Basin</b>											
					North	West					
CHAIN-106	313	ES	17/VIII/72	1500	51°32.2'	12°35.9'	19				
	321	ES	20/VIII/72	2890	50°12.3'	13°35.8'		1			
	323	ES	21/VIII/72	3356	50°08.3'	13°53.7'		10	6		
	326	ES	22/VIII/72	3859	50°04.9'	14°23.8'			11		
	328	ES	23/VIII/72	4426	50°04.7'	15°44.8'			13		
	330 <sup>new</sup>	ES	24/VIII/72	4632	50°43.5'	17°51.7'			11		
INCAL	DS-01	ES	15/VII/76	2091	57°59.7'	10°39.8'	2	141			
	DS-02	ES	16/VII/76	2081	57°58.8'	10°48.5'	1	23			
	CP-01	CP	16/VII/76	2040	57°57.7'	10°55.0'		13			
	CP-02	CP	16/VII/76	2091	57°58.4'	10°42.8'		2			
	CP-03	CP	17/VII/76	2466	56°34.0'	11°06.4'		1			
	CP-04	CP	17/VII/76	2483	56°33.2'	11°11.3'		2			
	DS-05	ES	18/VII/76	3503	56°28.1'	11°11.7'		172			
	DS-06	ES	18/VII/76	2494	56°26.6'	11°10.5'		215			
	DS-07	ES	19/VII/76	2884	55°00.7'	12°31.0'		3			
	DS-08	ES	19/VII/76	2891	55°02.0'	12°34.6'		55			
	CP-05	CP	19/VII/76	2884	55°00.4'	12°29.4'		22			
	CP-06	CP	19/VII/76	2888	55°02.3'	12°40.3'		6			
	DS-09	ES	20/VII/76	2897	55°03.7'	2°52.6'		74	1		

## PROCHAETODERMATIDAE—APLACOPHORA

489

CP-07	CP	20/III/76	2895	55°03.4'	12°46.2'	5	1	2
DS-10	ES	27/III/76	2719	50°12.7'	13°16.6'	2	1	1
CP-09	CP	27/III/76	2659	50°15.4'	13°15.8'	2	1	1
OS-01	ES	30/III/76	2634	50°14.4'	13°10.9'	2	1	1
WS-02	WS	30/III/76	2498	50°19.3'	12°55.8'	7	1	1
CP-10	CP	31/III/76	4823	48°25.5'	15°10.7'	4	4	4
DS-11	ES	1/III/76	4823	48°18.8'	15°11.5'	6	6	6
CP-11	CP	1/III/76	4823	48°20.4'	15°14.6'	3	3	3
WS-03	WS	1/III/76	4829	48°19.2'	15°23.3'	2	2	2
OS-02	ES	2/III/76	4829	48°19.2'	15°15.9'	1	1	1
CP-12	CP	4/III/76	4796	46°00.5'	10°18.3'	5	5	5
OS-03	ES	4/III/76	4798	46°02.5'	10°19.5'	5	5	5
OS-04	ES	5/III/76	4796	46°03.9'	10°12.8'	5	5	5
WS-05	WS	5/III/76	4804	46°03.0'	10°15.7'	1	1	1
DS-13	ES	6/III/76	4822	46°01.9'	10°17.9'	3	3	3
WS-07	WS	7/III/76	4281	47°30.6'	9°37.1'	4	4	4
WS-08	WS	9/III/76	4287	47°30.5'	9°33.7'	1	1	1
OS-06	ES	9/III/76	4316	47°27.3'	9°36.2'	5	5	5
DS-16	ES	9/III/76	4268	47°29.8'	9°33.4'	2	2	2
OS-07	ES	10/III/76	4249	47°31.8'	9°34.3'	26	26	26
WS-09	WS	10/III/76	4277	47°28.8'	9°34.0'	5	5	5
WS-10	WS	11/III/76	4354	47°27.3'	9°39.9'	2	2	2
OS-08	ES	11/III/76	4327	47°29.8'	9°39.2'	4	4	4
111-B16	n.d.	n.d.	4512	45°35.2'	7°51.6'	1	1	1
111-	n.d.	n.d.	4760	45°08'	5°31'	51	51	51
EO13	n.d.	n.d.	1175	47°33.4'	7°19.0'	1	1	1
THALASSA-73	GBS	22/X/73	1200	48°52.2'	11°07.0'	1	1	1
Z-445	PBS	27/X/73	1180	48°37.3'	9°53.0'	1	1	1
Z-459	GBS	29/X/73	4260	47°33.9'	9°18.4'	1	1	1
DS-45	ES	27/III/73	4230	44°26.8'	4°50.7'	1	1	1
DS-47	ES	31/III/73	4203	44°29'	4°54'	4	4	4
DS-48	ES	31/III/73	2124	44°08.9'	4°15.9'	1	1	1
DS-50	ES	1/X/73	2430	44°11.3'	4°15.4'	4	4	4
DS-51	ES	18/II/74	2006	44°06.3'	4°12.4'	5	5	5
DS-52	ES	18/II/74	4125	47°34.9'	9°40.9'	1	1	1
DS-55	ES	22/II/74	4050	47°33.7'	9°28.2'	2	2	2
DS-56	ES	23/II/74	3742	47°26.8'	9°07.2'	2	2	2
DS-60	ES	24/II/74						

NORATLANTE

THALASSA-73

BIOGAS-III

BIOGAS-IV



TABLE I (Continued)

Cruise or dive no. <sup>a</sup>	Station	Gear <sup>b</sup>	Date	Depth m	Latitude	Longitude	P younger	S clenchi	C turnerae	C gulosus	C scalpellu <sup>c</sup>
BIOGAS-V	DS-61	ES	25/II/74	2250	47°34.7'	8°38.8'		3			
	DS-62	ES	26/II/74	2175	47°32.8'	8°40'		1			
	DS-63	ES	26/II/74	2126	47°32.8'	8°35'		1			
	DS-64	ES	26/II/74	2156	47°29.2'	8°30.7'		2			
BIOGAS-VI	KR-33	KR	24/II/74	2963	47°30.4'	9°06.9'			1		
	KR-35	KR	25/II/74	4140	47°26'	9°08.7'			1		
	DS-66	ES	16/VI/74	3480	47°28.2'	9°—			6		
	DS-67	ES	17/VI/74	4150	47°31'	9°35'			5		
BIOGAS-VII	DS-70	ES	21/VI/74	2150	44°08.8'	4°17.4'		2			
	DS-77	ES	24/X/74	4150	47°31.8'	9°34.6'			1		
	DS-78	ES	25/X/74	4240	46°31.2'	10°23.8'			5		
	DS-79	ES	26/X/74	4706	46°30.4'	10°27.1'			6		
BIOGAS-VIII	DS-80	ES	27/X/74	4720	46°29.5'	10°29.5'			4		
	DS-82	ES	29/X/74	4462	44°25.4'	4°52.8'			1		
	DS-85	ES	30/X/74	4462	44°23.2'	4°50.8'			6		
	DS-86	ES	31/X/74	1950	44°04.8'	4°18.7'					
BIOGAS-IX	DS-87	ES	1/XI/74	1913	44°05.2'	4°19.4'		2			
	DS-88	ES	1/XI/74	1894	44°05.2'	4°15.7'					
	CP-14	CP	23/X/74	4237	47°32'	9°35.9'			10		
	CP-15	CP	25/X/74	4715	46°32.2'	10°28.5'			4		
BIOGAS-X	CP-16	CP	25/X/74	4825	46°27.3'	10°25.8'			2		
	CP-17	CP	26/X/74	4706	46°30.8'	10°19.5'			2		
	CP-19	CP	28/X/74	4434	44°24.9'	4°51.3'			3		
	CP-20	CP	29/X/74	4459	44°21.2'	4°51.4'			2		
BIOGAS-XI	CP-22	CP	30/X/74	4475	44°22.9'	4°54.8'			8		
	CP-22A	CP	30/X/74	4475	44°22.9'	4°54.8'			1		
	CP-25A	CP	1/XI/74	1894	44°05'	4°17'					
	KG-142	SBC	18/IV/79	2182	47°33.4'	8°39.7'		1			
BIOGAS-XII	KG-144	SBC	to	2225	47°34.2'	8°40.3'		1			
	KG-145	SBC	8/VI/79	2170	47°32.9'	8°39.1'		2			
	KG-157	SBC		2227	47°34.3'	8°39.8'		1			
	KG-173	SBC	16/IV/80	2740	47°31.6'	9°04.2'		1			
BIOGAS-XIII	KG-174	SBC	17/IV/80	2885	47°32.5'	9°05.5'		1			
	KG-178	SBC	18/IV/80	2770	47°32.1'	9°05.2'		1			
	KG-179	SBC	18/IV/80	2730	47°32.2'	9°04.5'		1			

## PROCHAETODERMATIDAE—APLACOPHORA

491

BIOGAS XI	KG-181	SBC	18/V/80	2811	47°31.5'	9°06.4'	2			
	KG-183	SBC	18/V/80	2748	47°31.5'	9°05.1'	1			
	KG-185	SBC	19/V/80	2828	47°32.0'	9°06.3'	1			
	KG-183	SBC	18/V/80	2748	47°31.5'	9°05.1'	1			
	KG-185	SBC	19/V/80	2828	47°32.0'	9°06.3'	1			
	KG-203	SBC	4/X/81	4210	47°34.9'	9°39.8'	2			
	KG-206	SBC	4/X/81	4130	47°35.2'	9°39.5'	1			
	KG-207	SBC	4/X/81	4135	47°35.3'	9°38.5'	6			
	KG-208	SBC	4/X/81	4130	47°35.0'	9°40.0'	4			
	KG-209	SBC	6/X/81	4190	47°34.4'	9°38.9'	3			
MAC 81 SARSIA	KG-210	SBC	7/X/81	4135	47°35.4'	9°39.2'	2			
	KG-211	SBC	7/X/81	4170	47°34.7'	9°39.1'	4			
	KG-212	SBC	7/X/81	4130	47°34.9'	9°39.3'	1			
	KG-213	SBC	7/X/81	4150	47°34.7'	9°39.0'	2			
	KG-215	SBC	7/X/81	4110	47°34.8'	9°39.9'	3			
	KG-216	SBC	7/X/81	4200	47°35.0'	9°38.5'	1			
	KG-218	SBC	8/X/81	4170	47°34.8'	9°40.3'	1			
	No. 14	Exp.	11 mo.	2120	47°33.4'	8°33.7'	1			
	65	ES	25/VII/67	1922	46°15'	4°50'	1			
	DISCOVERY	6710	ES	19/III/68	2670	27°23.6'	15°39.6'	4		
6711		ES	19/III/68	2988	27°14.9'	15°36.3'	1			
ATLANTIS II-31	142	ES	5/II/67	1624	10°30.0'	17°51.5'	19			
	145	ES	6/II/67	2185	10°36.0'	17°49.0'	9			
ATLANTIS II-42	195	ES	19/V/68	3797	14°49'	9°36'	5			
	198	ES	21/V/68	4559	10°29'	9°04'	1			
	199	ES	22/V/68	3764	9°47'	10°29'	4			

TABLE 1 (Continued)

Cruise or dive no. <sup>a</sup>	Station	Gear <sup>aa</sup>	Date	Depth m	Latitude	Longitude	P. yongei	S. clenchii	C. lumerae	C. gossion	C. scalpulum
200	ES	ES	22/IV/68	2644	9°41'	10°55'		4			1
201	ES	ES	22/IV/68	1964	9°29'	11°34'					22
202 <sup>aaa</sup>	ES	ES	23/IV/68	1427	9°05'	12°17'	3				59 <sup>aaa</sup>
DS-18	ES	ES	22/VI/71	4079	6°37.5'	8°18.2'			4		
Namibia Basin											
South											
ATLANTIS II-42	191	ES	17/IV/68	1546	23°05'	12°31.5'	66				
194	ES	ES	17/IV/68	2864	22°54'	11°55'		5			
DS-04	ES	ES	9/VI/71	4184	21°57.5'	9°22.7'			6		
DS-08	ES	ES	22/VI/71	3777	21°58.6'	10°16'			3		
TOTAL SPECIMENS							3122	1480	538	19	102

<sup>a</sup> Woods Hole Oceanographic Institution cruises: ATLANTIS, ATLANTIS II, CHAIN, KNORR, OCEANUS, Woods Hole Oceanographic Institution dives: ALVIN, Centre National de Tri d'Océanographie Biologique (Brest) cruises: INCAL, NORATLANTE, THALASSA, BIOGAS, MAC, WALDA, National Institute of Oceanography (U.K.) cruises: SALSIA, DISCOVERY

<sup>aa</sup> Quantitative gear, lowered on wire from shipboard: AD—anchor dredge (0.40–1.00 m<sup>2</sup>), SBC—spade box corer (0.25 m<sup>2</sup>), KR—Remek corer (600 cm<sup>2</sup>), manipulated from submersible.

BEB—Birge-Elman box corer (25 m<sup>2</sup>, 44.5 m<sup>2</sup>), TC—tube corer (35 cm<sup>2</sup>), BC—box corer (225 cm<sup>2</sup>), Nonquantitative samplers: ES—epibenthic sled trawl, CP—perch trawl, WS—Wormley trawl, GBS, PBS—large, small Boillor sled trawls. Experimental boxes: Exp.

<sup>aaa</sup> Type locality.

† Only inner 90 cm<sup>2</sup> of box core sorted.

TABLE II

*Material examined, Pacific Ocean (Chevroderma whitlatchi)*

Cruise or dive no.*	Station or core	Gear**	Date	Depth m	Latitude north	Longitude west	No.
Aleutian Trench							
SEVENTOW Leg 7	H-39	SBC	20/VII/70	7298	50°58.0'	171°37.5'	31
Off Oregon							
Oregon State U.	AD-136	AD	9/II/65	2800	44°50.9'	127°34.1'	1
Off Baja California							
MELVILLE 70- III-1	n.d.	n.d.	21/III/70	3950	31°47.0'	120°14.8'	1
Panama Basin							
ALVIN 1132, 1230-32, 1234-39	***	BC	9/IX/81- 14/VI/ 82	3912	5°20.7'	81°56.2'	31***
Near Galapagos Vents							
GILLISS-301	Core 14	SBC	18/II/79	2730	00°35.0'	86°05.7'	1
Mid-Pacific							
DOMES Proj.	48-22	SBC	n.d.	5117	8°16.0'	151°11.3'	2
	53-45	SBC	n.d.	4985	11°43.9'	138°22.2'	1

\* Scripps Institution of Oceanography cruises: SEVENTOW, MELVILLE 70; Woods Hole Oceanographic Institution dives: ALVIN; Galapagos Biology Expedition cruise: GILLISS; U.S. National Oceanographic and Atmospheric Administration project: DOMES.

\*\* See footnote, Table I.

\*\*\* Type locality

and radulae are designated as paratypes; for most illustrated paratypes there are permanent slides of spicules and radulae.

#### TAXONOMIC CHARACTERS

The taxonomy of the Aplacophora has in the past relied primarily on interpretation of histological sections, and most species descriptions have been based on one or a few specimens. The results have not made for easily accessible or recognizable characters for purposes of identification. Radulae and spicules have seldom been adequately figured, and no studies exist that rigorously describe intraspecific variation within a species.

The acquisition of large deep-sea benthic samples over wide geographic areas since the early 1960s has made numerous specimens available for studying aplacophoran species both between and within populations. The insights gained from these large and numerous samples have shown that for the Prochaetodermatidae, hard parts and

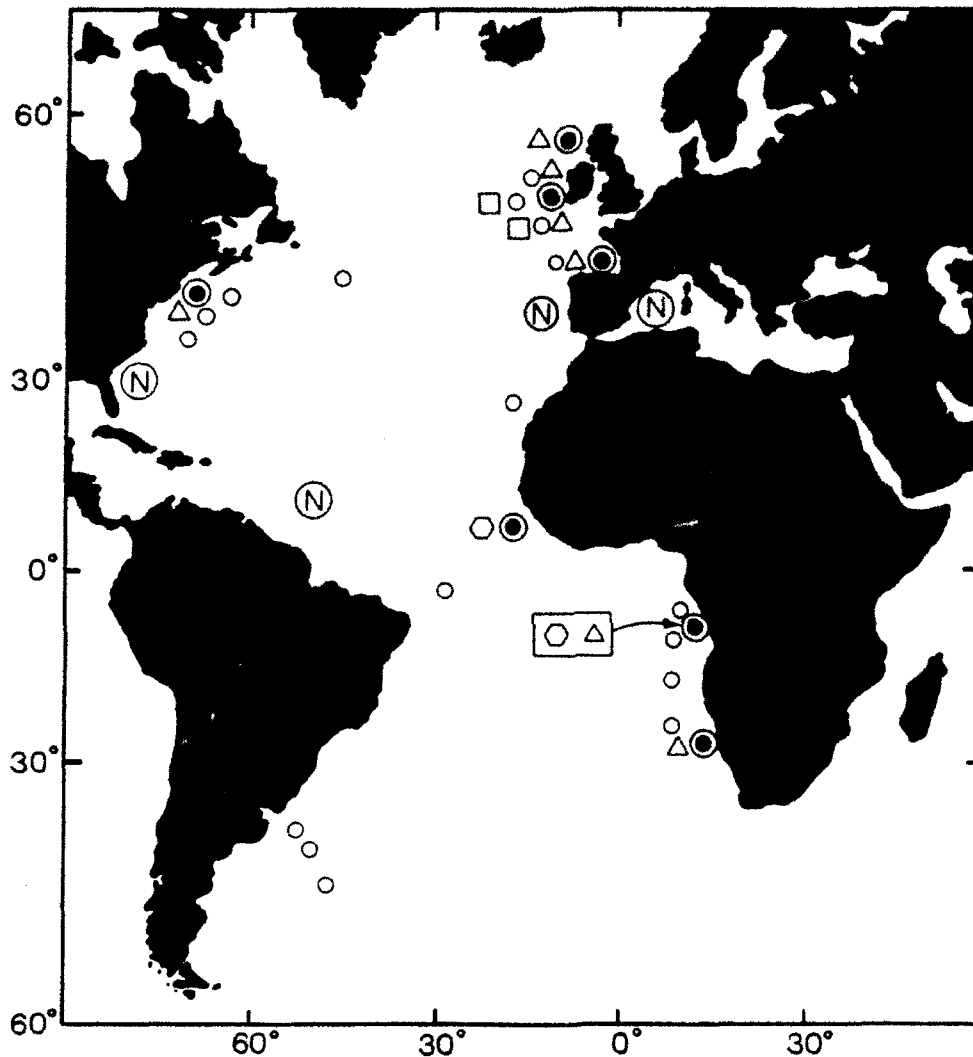


FIGURE 1. Distribution of *Prochaetoderma yongei* (solid, ringed circle), *Spathoderma clenchi* (triangle), *Chevroderma turnerae* (open circle), *C. gauson* (square), and *C. scalpellum* (hexagon). Data generalized from about 165 stations listed in Table I. Circled N, area sampled in which none of the five species occurred.

external morphologies characterize species, and that the morphology of spicules determines affinities and defines genera in this family.

No internal soft anatomy has been used here to describe species because of the great histologic similarity among species and because the size and arrangement of internal organs is reflected in the body shape.

#### *Body shape*

The body of the Prochaetodermatidae is cylindrical and divided into three regions: anterium, trunk, and posterium (Fig. 2A). The *anterium* bears the oral shield and few

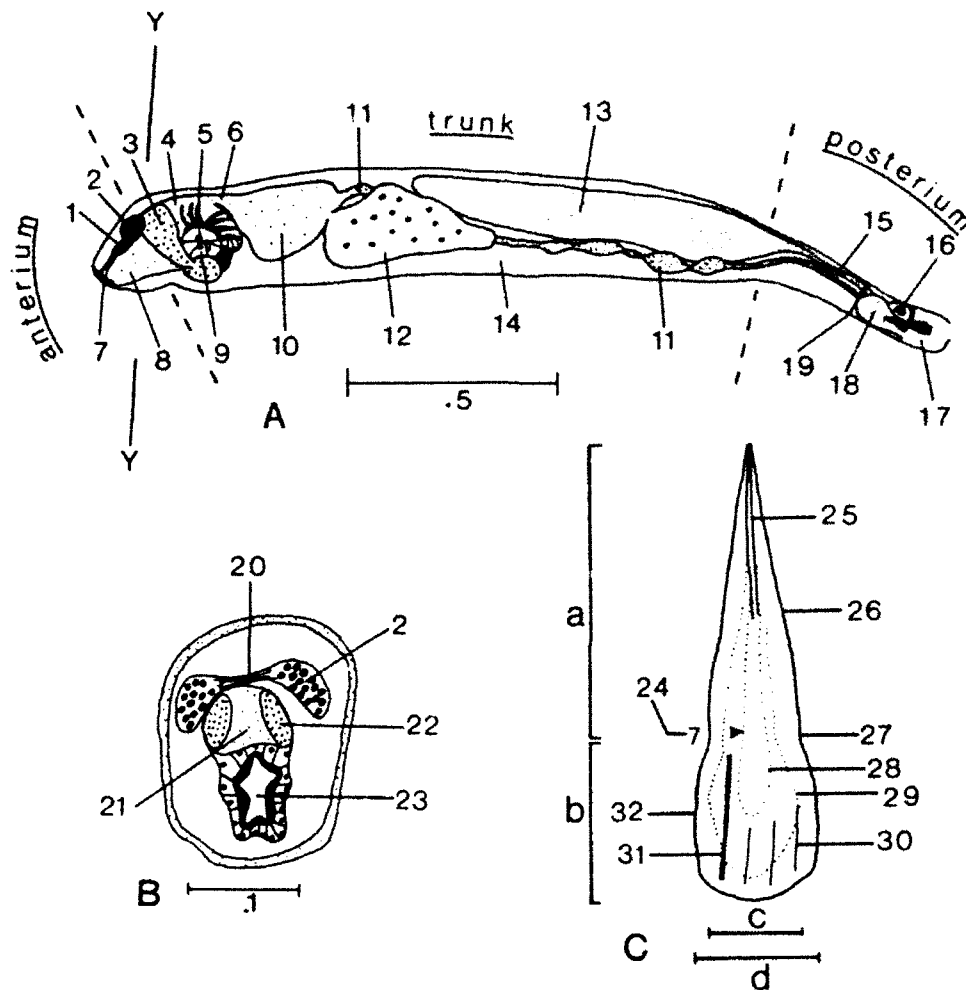


FIGURE 2. A. Genus *Prochaetoderma*, generalized anatomy, semi-diagrammatic. Dashed lines indicate boundaries between body regions. B. Cross-section through Y-Y in diagram A showing distal ends of jaws and separated lobes of cerebral ganglia joined by thick commissure. C. Morphological characters of a spicule. 1 precerebral ganglion, 2 cerebral ganglion, 3 jaw, 4 buccal cavity, 5 radula, 6 esophagus, 7 oral shield, 8 oral cavity, 9 chondroid-like bolster, 10 stomach, 11 intestine, 12 digestive gland, 13 gonad, 14 hemocoel, 15 gonopericardial duct, 16 heart within pericardium, 17 cloaca or mantle cavity with gill, 18 coelomoduct, 19 vertical posterior septum, 20 cerebral commissure, 21 sheet of cuticle joining distal ends of jaw, 22 distal end of jaw, 23 cuticle-lined oral cavity, 24 greatest spicule thickness in micrometers indicated by arrowhead and numeral, 25 keel or heavy ridge, 26 blade edge, 27 waist, 28 and 29 isochromes, 30 fine ridge, 31 groove, 32 base edge, *a* blade length, *b* base length, *c* maximum blade width, *d* maximum base width.

spicules and is often inflated; it may be retracted and introverted in preserved specimens. The *trunk* is set off from the anterior by a much greater density of spicules. The *posterior* is narrower than the trunk and often elongate and tail-like; the exact demarcation between trunk and posterior is sometimes difficult to establish.

Measurements of the trunk and posterior allow quantification of the variation in body shape among populations of a single species, as well as differentiating body shape among species.

*Oral shield*

The paired oral shield varies in size among species of Prochaetodermatidae (Fig. 3); size is also related to specimen size within a species and thus must be used cautiously as a taxonomic character. The relative sizes among species can be compared quanti-

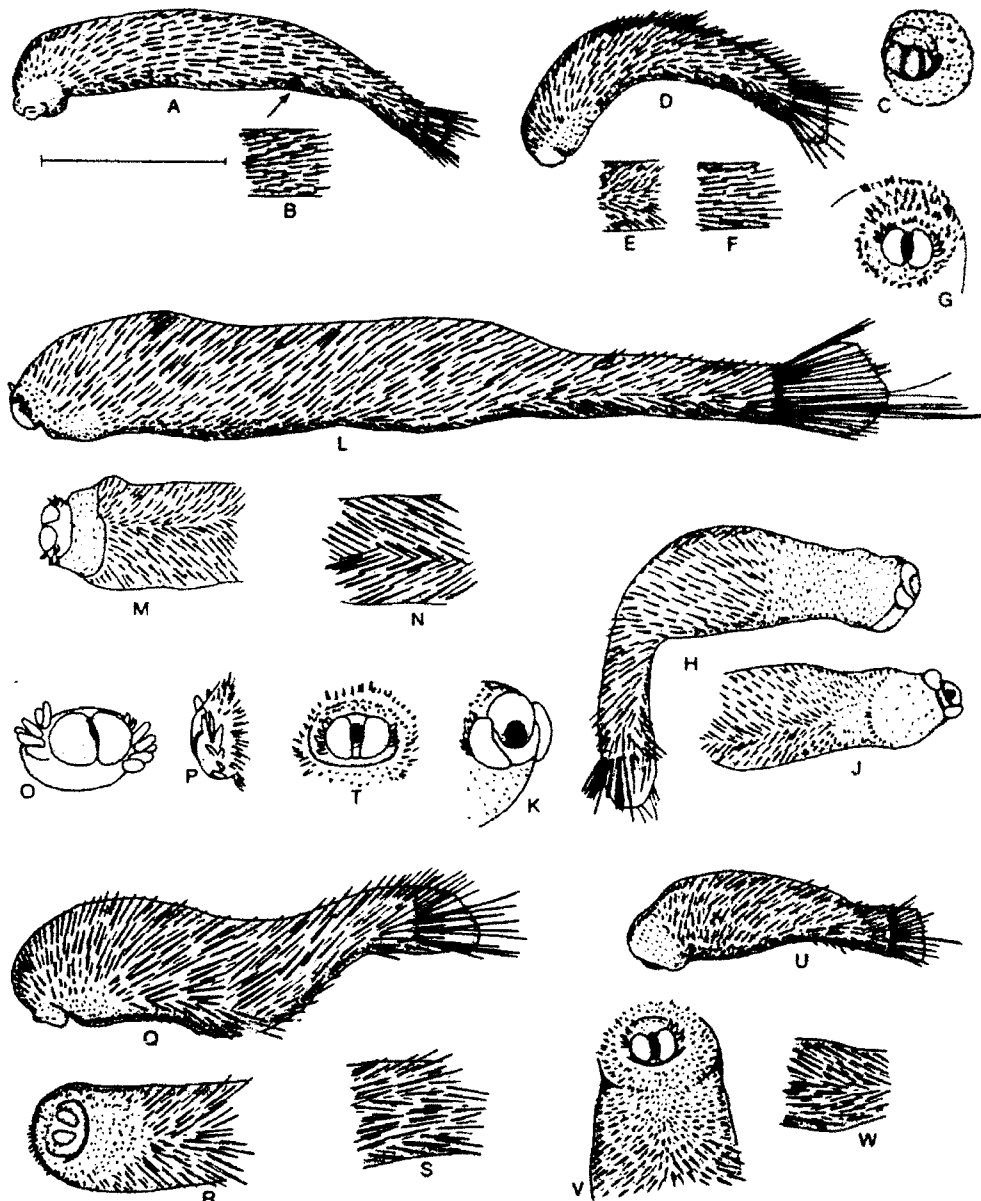


FIGURE 3. Holotypes. A-C. *Prochaetoderma yongei* n. sp. D-G. *Spathoderma clenchi* n.g. n. sp. H-K. *Chevroderma whitlatchi* n.g. n. sp. L-P. *Chevroderma turnerae* n. sp., genus type. Q-T. *Chevroderma gauson*, n. sp. U-W. *Chevroderma scalpellum* n. sp. Distribution of spicules, mid-dorsal view: B, F, N, S, W; mid-ventral view: E, M, J, R, V. Scale line equals 0.5 mm for oral shield illustrations C, G, K, O, P, T, and V; for all remaining illustrations it equals 1.0 mm.

tatively by using the following index: (length  $\times$  width of oral shield)  $\div$  (trunk diameter)  $\times$  100. This index is given for holotypes.

There may be relatively large, possibly tactile oral-shield spicules just lateral to the oral shield (Figs. 3G, K, O, P); they are lacking or indistinct in some species (Fig. 3C).

#### *Cloaca, or mantle cavity*

The posterior end of the body is rounded or truncated in lateral view, the shape depending on the cloacal wall musculature which closes off the mantle cavity (Fig. 3).

#### *Spicules*

*Attitude.* According to species, spicules are carried flat against the body or bent outwards from it. They may be arranged with the long axis parallel to the body axis (Fig. 3A) or obliquely with the proximal end ventral to the distal end (Fig. 3L). A species may be translucent or opaque according to spicule thickness and attitude. The morphology of the spicules and body wall musculature determine the attitude of spicules relative to the body wall.

*Morphology.* The morphology of individual spicules is the taxonomic character most useful for distinguishing species and for determining relationships among species. A spicule has a *base* (Fig. 2C), which lies within the cuticle and is anterior in position to the *blade*, which is external to the cuticle; the base is usually set off from the blade by a *waist*. The blade may have a *keel* on the frontal surface; *ridges* or *grooves* may be present on either the blade or base. Spicules may be symmetrical or asymmetrical. Symmetry is revealed by interference colors seen under cross-polarized light. Spicules may lie flat in one plane, or the blade may be rotated about the long axis to a plane different from that of the base or it may be bent at the waist towards the body or away from it.

Spicules vary in their morphology both along the body from anterior to posterior and from the ventral to the lateral and dorsal sides; thus they are here described from particular regions of the body, which are indicated on a drawing of the specimen from which the spicules were taken (Figs. 6–13). However, dorsal spicules at the junction of the trunk and posterium are usually adequate for species determination and their morphology alone is given under the diagnosis for each species.

#### *Radula and jaws*

The jaws and radula of the family Prochaetodermatidae have been described by Kowalevsky (1901) and Scheltema (1981). There is great morphological similarity among species in these structures, the greatest differences lying in size of jaws and teeth and in shape and length of the central plate (Figs. 14, 15). No statistically significant correlations were found in mature specimens of two species (a) between specimen length and either tooth or jaw length, or (b) between tooth length and jaw length. The ranges in ratios of tooth length to jaw length are similar in all six species described here.

The jaws can usually be seen *in situ* within a specimen viewed with transmitted light and thus family membership determined without dissection.

### SYSTEMATIC ACCOUNT

#### Family Prochaetodermatidae Salvini-Plawen 1969

The Prochaetodermatidae are Chaetodermomorpha (= Caudofoveata), or burrowing, footless solenogasters, uniquely characterized by the presence of a pair of



large, cuticular jaws and the morphology of a small distichous radula. The cuticle of the jaws is discrete from the buccal cavity cuticle (Scheltema, 1981); it is bound by basement membrane and not produced by preradular, lateral pouches as stated in Boss (1982). The radula is formed of 8 to 12 rows of paired teeth on an undivided radular membrane; between each pair is a central plate. A lateral, tooth-like projection of the radular membrane lies alongside each tooth (Fig. 15 upper left tooth, Scheltema, 1981, Figs. 7D, 11A). Each tooth has a lateral membranous "wing" and a membranous median extension, or brush, bearing many serrations (Figs. 4E, 15). The distal teeth are worn (Scheltema, 1981, Fig. 11B). The odontophore bolsters are chondroid-like (Fig. 2A; Scheltema, 1978, Fig. 3B).

All prochaetodermatid species are small, usually less than 5 mm in body length, and thicker anteriorly than posteriorly. Although the body is cylindrical, the dorsal and ventral surfaces are distinct: the spicules diverge away from the ventral midline and the body of contracted specimens is usually flexed into an arch, the dorsal side uppermost. The oral shield is divided into two lateral parts with or without lateral spicules. The epidermal spicules are solid, with ornamentation simple or lacking; the base is flat in cross-section and embedded in the epidermal cuticle, the blade is flat, oval, or triangular to round in cross-section and extends beyond the cuticle. Paired groups of long, lateroventral spines trail posteriorly beyond the cloaca (Figs. 3L, U) but are often broken off in preserved specimens.

Three distinct body regions reflect internal anatomy (Fig. 2A): (1) the antenum is a hemocoelic space surrounding an expansible oral cavity into which can be protruded the jaws and buccal mass (Fig. 10, specimen), (2) a broad trunk, with weak body-wall musculature, contains the paired lobes of the cerebral ganglion with their thick commissure (Fig. 2B), buccal mass, stomach, digestive gland, anterior intestine, and gonad, and (3) a narrow posterior, with strong longitudinal muscles, contains the posterior intestine, unpaired gonoduct (paired in other chaetodermatids), heart, pericardium, paired coelomoducts, and, posteriorly, a small cloaca with a pair of gills, each formed of two lamellae (Salvini-Plawen, 1969, Fig. 12). The stomach is unique among the Chaetodermomorpha in lacking a dorsal ciliated typhlosole, and it has no locally thickened cuticle; the digestive gland is uniquely without a dorsal band of granular cells (Scheltema, 1981). The members of the family are dioecious; in translucent species, sex can often be determined without dissection.

Except in the Scandinavian fjords, Arctic, and Antarctic where they have not been reported, the Prochaetodermatidae are ubiquitous in soft oceanic sediments from 50 to over 7000 m.

#### Genus *Prochaetoderma* Thiele

*Prochaetoderma* Thiele 1902, *Zeit. Wiss. Zool.* 72II: 275.

With characters of the family. Spicules flat; base shorter than blade, blade broad and triangular with median keel and sharp distal point.

Distribution: Atlantic Ocean and Mediterranean Sea, 50–2000 m.

Type species: *Chaetoderma radulifera* Kowalevsky 1901, by monotypy; Sea of Marmara.

#### *Prochaetoderma raduliferum* (Kowalevsky)

*Chaetoderma radulifera* Kowalevsky 1901, *Arch. Zool. Exp.*, ser. 3, 9: 264–274, Figs. 1–20. Sea of Marmara, Isle des Princes, 35–40 fms. [Type specimen unknown; type figure, here designated, Pl. 10, Fig. 3; redrawn herein, Fig. 6].

*Prochaetoderma raduliferum*. Salvini-Plawen, 1972, pp. 37–39, Figs. 10–12 in *Fifth European Marine Biology Symposium*, B. Battaglia, ed. Piccin Editore, Padova.



FIGURE 4. Scicules of *Prochaetoderma yongei* n. sp. (A–C) and *Spathoderma clenchi* n.g., n. sp. (D, F); radula tooth (E) of an unnamed species of Prochaetodermatidae. A. *P. yongei* holotype, 1470 m, North American Basin (cf. Fig. 6); B. *P. yongei*, 805 m, North American Basin (CH-88 Sta. 207) (cf. Fig. 7); C. *P. yongei*, 1546 m, Namibia Basin (All-42 Sta. 191) (cf. Fig. 8); D. *S. clenchi* holotype, 2178 m, North American Basin (cf. Fig. 9); F. same as D, detail of blade. Scale lines equal 20 μm.

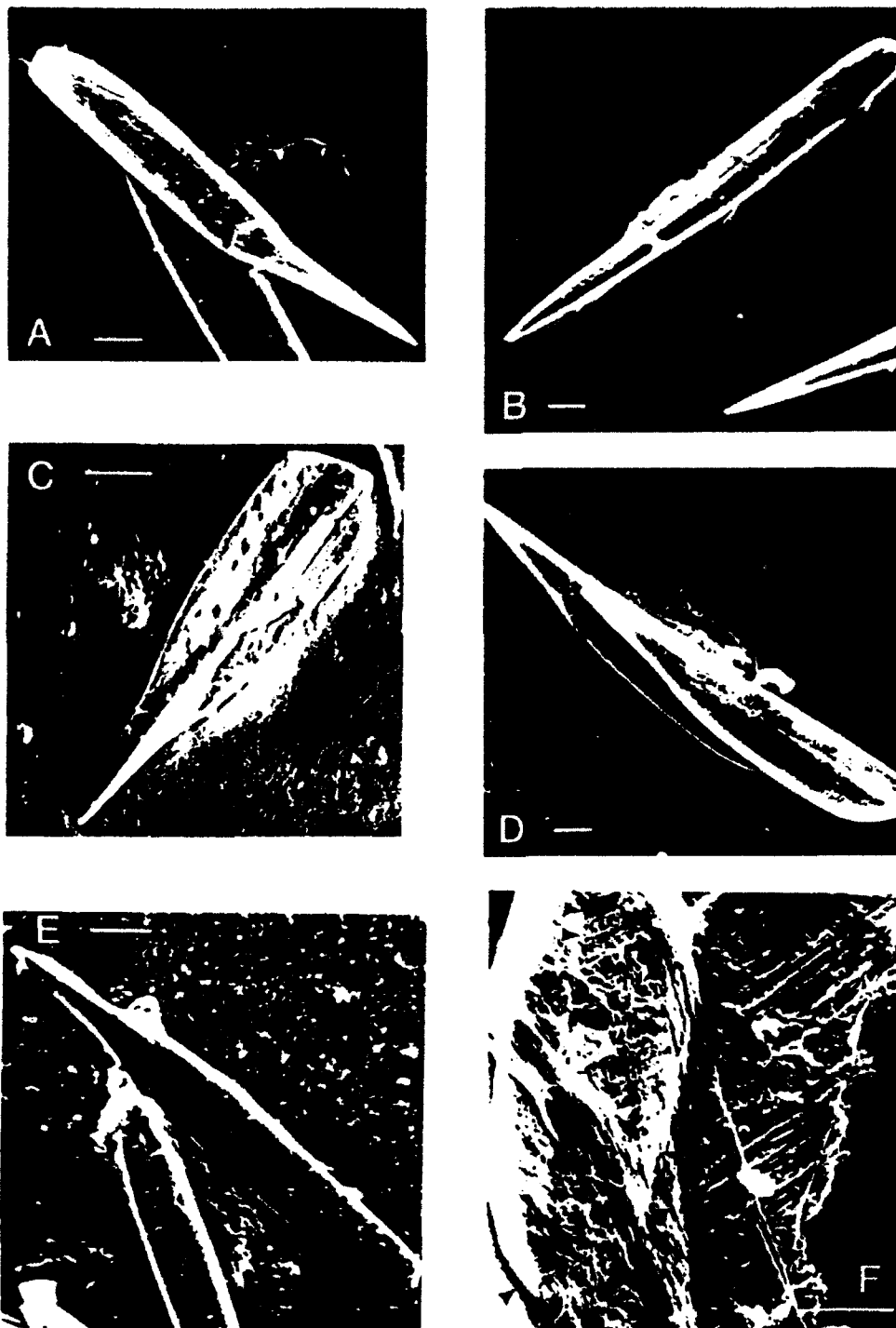


FIGURE 5. Spicules of four species of *Chevroderma* n.g. A. *C. gausson*, paratype no. 5, 4829 m, West European Basin (cf Fig. 11); B. *C. turnerae*, holotype, 4,833 m, North American Basin (cf Fig. 10); C. *C. scalpellum*, paratype no. 1, 1427 m, Angola Basin (cf Fig. 12); D. *C. turnerae*, paratype no. 5, 4237 m, West European Basin (cf Fig. 10 W spicule 4); E. *C. whilatchi*, paratype no. 2, 7298 m, Aleutian Trench (cf Fig. 13); F. *C. turnerae*, paratype no. 5, showing spicule embedded in crossed fibers of cuticle, arrowheads point to edge of spicule and longitudinal groove. Scale lines equal 20  $\mu$ m.

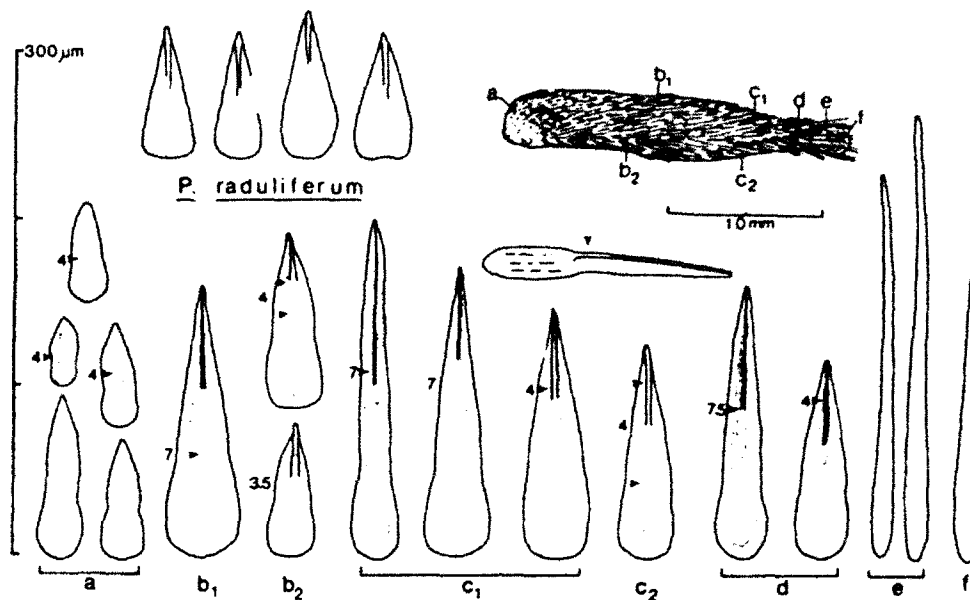


FIGURE 6. Upper left: spicules of *Prochaetoderma raduliferum* (Kowalevsky 1901) redrawn from type figure (pl. 10, Fig. 3); scale of original drawings not certain, scale used here from Salvini-Plawen (1972, Fig. 12 d, f). Lower rows: spicules of *Prochaetoderma yongei* n. sp. paratype no. 1, 1470 m, North American Basin (type locality). Spicules a-f from body regions indicated on figured specimen, above right; spicule below specimen, lateral view of a trunk spicule showing blade slightly offset outwards from base (arrowhead).

*Prochaetoderma raduliferum*. Salvini-Plawen, 1977, *Vie Milieu* 27: 56-63, Figs. 3-5; *Bull. Mus. Nat. Hist. Nat., Paris* (ser. 3), 447 (Zool. 310): 417, Table I.  
Distribution: Sea of Marmara; eastern and western Mediterranean; 54-2415 m.

*Prochaetoderma yongei* n. sp.

Figs. 1, 3A-C, 4A-C, 6, 7, 8, 14 y<sup>1</sup>-y<sup>3</sup>; Tables I, III, IV, V, VII

*Prochaetoderma* sp. Grassle, 1977, *Nature* 265: 618-619, Table 2.

*Prochaetoderma* sp. Scheltema, 1978, *Malacologia* 17, Figs. 1A, 3B, 5C.

*Prochaetoderma* sp. y. Scheltema, 1981, *Malacologia* 20, Figs. 2E-G, 3D-H, K, 7D-F, 11A-C (non 7A-C, caption in error).

*Prochaetoderma* sp. B. Scheltema, 1985, in L. Laubier and C. Monniot, eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS*, IFREMER, Brest, pp. 391-396, Tables 1, 2.

**Diagnosis:** Translucent, slender; spicules flat-lying, parallel to long axis of body; less than 3 mm long, posterium  $\frac{1}{4}$  total length; posteroventral thickened cuticular patch present; oral shield small, oral shield spicules not distinct; spicules straight, sharply keeled, indented at waist, blade with convex sides, base flared proximally, greatest length 252  $\mu$ m; greatest jaw length 365  $\mu$ m; radula tooth length up to 90  $\mu$ m; central radula plate short and relatively broad with ends directed posteriorly, greatest length 26  $\mu$ m.

This species is named in honor of Sir Maurice Yonge, whose book *The Seashore* early led me to the study of marine animals.

Holotype: North American Basin, 39°46.5'N, 70°43.3'W, 1470–1330 m (ATLANTIS II-12, Sta. 73, 25/VIII/64). USNM No. 850201.

**Illustrated paratypes:**

Nos. 1, 4: Type locality, USNM Nos. 850202 (No. 1), 850208 (No. 4).

No. 2: Namibia Basin, 23°05'S, 12°31.5'E, 1546–1559 m (ATLANTIS II-42 Sta. 191, 17/V/68). USNM No. 850204.

No. 3: North American Basin, 39°51.3'N, 70°54.3'W, 805–811 m (CHAIN-88 Sta. 207, 21/II/69). USNM No. 850206.

*Description*

**External morphology.** *Prochaetoderma yongei* is a small, slender, translucent species with flat-lying spicules oriented anterior-posterior except where they diverge along the ventral midline (Fig. 3A, B). Oral shield spicules are indistinct. The total body length averages 1.5 to 2.1 mm in seven populations; the greatest length is 2.8 mm. Trunk diameter averages 0.3 to 0.4 mm, with greatest diameter 0.6 mm. The posterium is about ¼ total length; it averages 0.4 to 0.5 mm in length and 0.2 mm in diameter and ranges up to 1.0 mm by 0.3 mm. The mean index of posterium length to trunk length averages 0.31 to 0.35 in seven populations, but the range is great, from 0.18 to 0.68. An opaque, thickened patch of cuticle at the ventral junction of the trunk and posterium is characteristic of the species (Fig. 3A, arrow). The oral shield is small (Fig. 3C); the cloaca is rounded.

Holotype: Male; total length 2.6 mm; trunk 2.0 by 0.4 mm; posterium 0.6 by 0.2 mm; index of posterium to trunk 0.30. Oral shield 0.05 by 0.09 mm; index of oral shield to trunk diameter 1.12.

**Spicules.** A median keel runs the length of the blade; it is sharpest and most distinct distally (Figs. 4A–C, 6, 7, 8) and is lacking in anteriormost and posteriormost spicules from regions *a*, *e*, and *f*. Other ornamentation on the blade is lacking except in region *b*<sub>1</sub> from specimens in the Namibia Basin, which have short ridges parallel to the keel (Fig. 8). The spicule base is flared proximally with convex sides and sometimes faint ridges; occasionally the base has straight sides which are either flared or parallel. The proximal end is usually rounded, but may be straight or broadly triangular. The blade usually has convex sides proximally; it is distinctly set off from the base by an indentation at the waist. Some blades have straight sides, particularly in juveniles (Fig. 7D). Distally the sides of the blade straighten or become slightly concave before tapering to a sharp point. The isochromes are symmetrical. Spicules from the anterior end of the body are thickest at the proximal part of the blade just above the waist (region *b*<sub>1</sub>); further posteriorly, they are thickest more distally (regions *c* and *d*). In lateral view the base and blade are nearly straight, with the blade somewhat offset outwards from the base and slightly bent towards the body. Spicules from the ventral side of the body are thinner and shorter than those from the lateral and dorsal sides, and often the keel extends like a needle beyond the sides of the blade (regions *b*<sub>2</sub>, *c*<sub>2</sub>). Very short, very thin (2 μm) triangular spicules occur sparsely.

Ranges in dimensions of spicules from region *c* for eight populations in five ocean basins are shown in Table III.

The spicules of *P. yongei* differ from those figured by Kowalevsky (1901) for *P. raduliferum* in having a longer blade and a distinct waist (Fig. 6). The sides of the

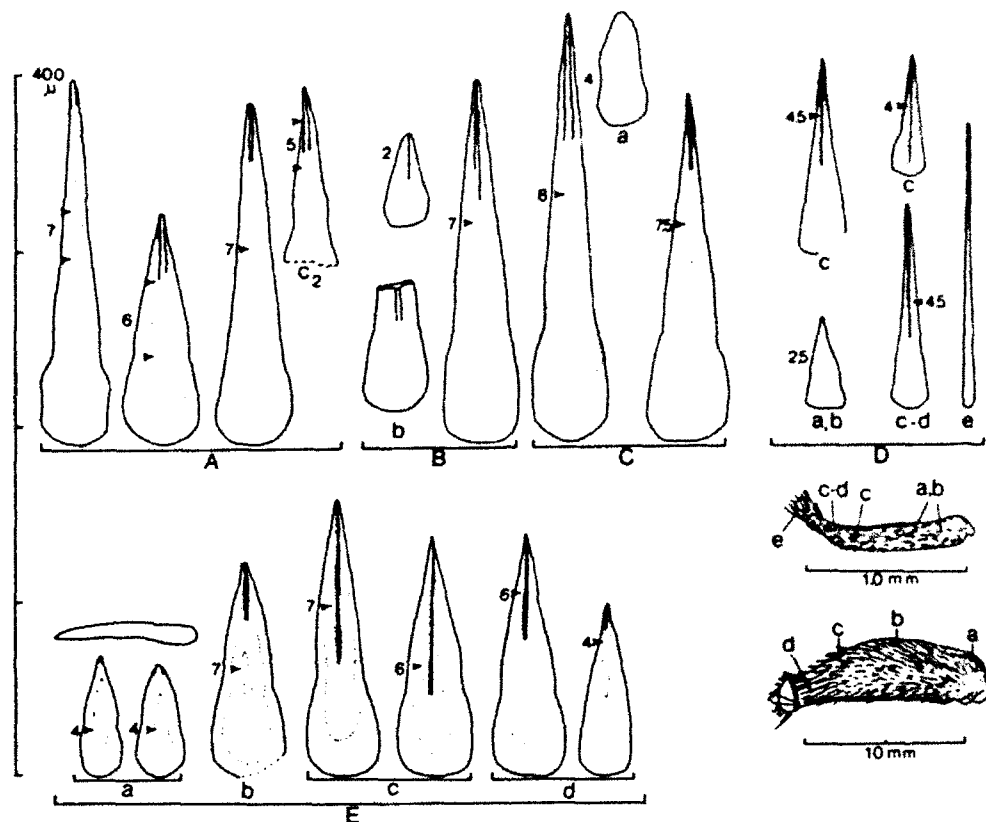


FIGURE 7. Variation in spicule morphology of *Prochaetoderma yongei* n. sp. from the North American Basin. A–C. spicules from junction of trunk and postterium, unless indicated otherwise; A. from single specimen from 805 m (CH-88 Sta. 207); B. from 3 specimens from 1470 m (type locality); C. from single specimen from 530 m (CH-58 Sta. 105); D. spicules from paratype no. 4, figured just below, immature specimen (type locality); E. spicules from paratype no. 3 figured at lower right, a short, stubby specimen from 805 m (CH-88 Sta. 207).

blade are straight in *P. raduliferum* and convex in *P. yongei*; the base in *P. raduliferum* is round, and in *P. yongei* it is flared proximally.

**Radula and jaws.** The jaws and teeth are typical for the family and small (Fig. 14  $y^1$ – $y^3$ ). Tooth length ranges up to 90  $\mu$ m; jaw length and width range up to 365 and 128  $\mu$ m, respectively. The entire radula has 8 to 11 rows of teeth. The central radula plate is short, up to 26  $\mu$ m, and broad, up to 8  $\mu$ m; the ends are directed posteriorly.

#### Morphological variation

Several populations of *Prochaetoderma yongei*, identified by similarity of spicule and radula morphology, were examined to determine the variability that occurs within this species and could therefore be expected in other species of the family Prochaetodermatidae.

**Spicules.** Several spicules from the dorsal junction of trunk and postterium were drawn and compared for 24 specimens from four stations along the Gay Head-Bermuda transect in the North American Basin and from five stations between the northern

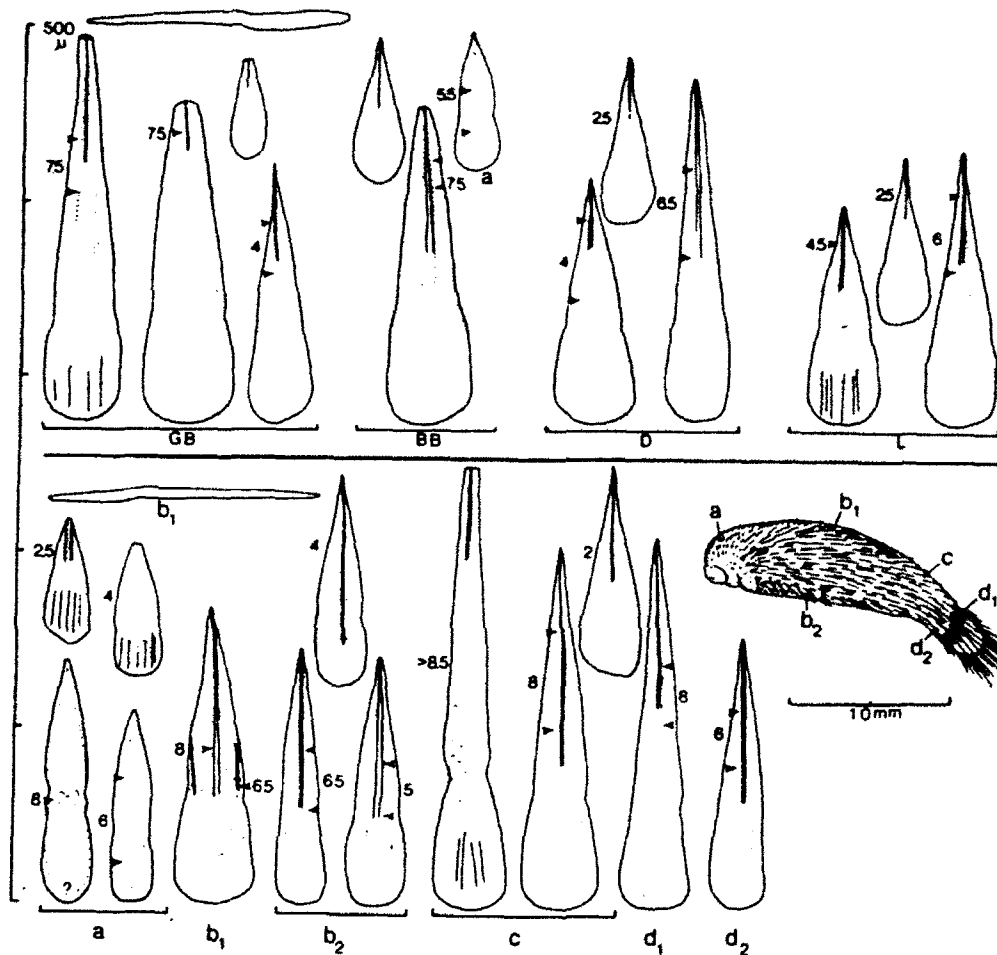


FIGURE 8. Variation in spicule morphology of *Prochaetoderma yongei* n. sp. from the eastern Atlantic. Upper row: spicules from junction of trunk and posterium, unless otherwise indicated. GB, off Great Britain (West European Basin), 2091 m (INCAL DS-01); BB, Bay of Biscay (West European Basin), 1922 m (SARSIA 65); D, Cape Verde Basin, 1624 m (All-31 Sta. 142); L, Angola Basin, 1427 m (All-42 Sta. 202). Lower row: spicules from paratype no. 2, 1546 m, Namibia Basin. Upper and middle left, lateral views showing offset blade.

West European Basin and Namibia Basin in the eastern Atlantic; spicules were measured from fifteen of these specimens (Table III) and scanning electron photomicrographs were made of spicules from three (Fig. 4A–C). Variation in shape is as great among spicules from a single specimen (Fig. 7A) as among spicules from far-distant populations (e.g., Namibia Basin at 1546 m, Fig. 8, lower row, and North American Basin at 530 m, Fig. 7C). Greatest blade length decreases with depth in the western Atlantic and from north to south in the eastern Atlantic between the West European Basin and Angola Basin; in the Namibia Basin, blade length again increases (Table III, Fig. 8).

Spicule length is not correlated with body length, except that very small juveniles have relatively small spicules (Fig. 7D). In a test of significance, the longest spicule

TABLE III

Range in spicule dimensions from body region c, in *Prochaetoderma yongei* and *Spathoderma clenchi* ( $\mu\text{m}$ ) (number of specimens in parentheses)

	Total length	Blade length	Base length	Blade width	Base width
<i>P. yongei</i>					
<i>No. American Basin</i>					
AII-12 Sta. 73 (6) (1400 m)	101-207	60-148	38-70	20-34	27-47
CH-88 Sta. 207 (3) (800 m)	128-202	81-158	40-61	22-32	34-45
CH-58 Sta. 105 (1) (500 m)	202-241	148-178	54-63	27-32	40-50
<i>West European Basin</i>					
INCAL DS-01 (1)	151-225	99-164	45-63	22-43	34-52
SARSIA 65 (1)	184-220	112-153	68-72	32-36	47-50
<i>Cape Verde Basin</i>					
AII-31 Sta. 142 (1)	144-198	88-142	56	25-29	38-47
<i>Angola Basin</i>					
AII-42 Sta. 202 (1)	126-162	74-108	50-52	29-32	40-43
<i>Namibia Basin</i>					
AII-42 Sta. 191 (1)	178-252	122-173	50-79	29-34	40-45
<i>S. clenchi</i>					
<i>No. American Basin</i>					
AII-30 Sta. 131 (1) (2178 m)	101-202	43-119	68-90	22	27-43
AII-12 Sta. 73 (4) (1400 m)	128-232	56-155	72-90	16-25	34-50
<i>West European Basin</i>					
INCAL DS-01 (1)	122-232	54-146	68-86	11-22	32-45
<i>Namibia Basin</i>					
AII-42 Sta. 194 (1)	142-227	74-130	56-97	22	25-43

from a specimen was not correlated with specimen length in nine North American Basin specimens from 1470 m (AII-12 Sta. 73,  $r = .25$ ) and in 6 specimens from 805 m (CH-88 Sta. 207,  $r = .36$ ). In the specimens from the 805 m station mean body length was 1.6 mm and greatest length of spicules was 202  $\mu\text{m}$ , whereas the mean body length of the specimens from 1470 m was significantly greater, 2.1 mm ( $P < .02$ ), but greatest spicule length was about the same, 207  $\mu\text{m}$ . On the other hand, in the eastern Atlantic, body length of a specimen from 2091 m off Scotland (INCAL



DS-01) was 1.6 mm and greatest spicule length 225  $\mu\text{m}$ , whereas a specimen of the same body length from 1427 m in the Angola Basin (All-42 Sta. 202) had spicules with greatest length of only 162  $\mu\text{m}$  (Fig. 8GB and L).

It is concluded that spicule shape and ornamentation, but not size, are of taxonomic significance in defining a widely distributed species of Prochaetodermatidae.

**Radula.** Jaws and radulae of 20 specimens ranging in length from 1.1 to 2.5 mm were examined, 19 from the North American Basin and 1 from the Namibia Basin. Of the former, 6 were from short, stubby specimens at 805 m and 13 from long, slender specimens at 1470 m (*cf.*, specimens in Figs. 6 and 7). For the North American Basin, greatest jaw length at 805 and 1470 m depths was 365 and 360  $\mu\text{m}$ , respectively; greatest tooth length, 90 and 85  $\mu\text{m}$ ; and greatest length of the central plate, 25 and 26  $\mu\text{m}$ . In the specimen from the Namibia Basin, jaw length was 336  $\mu\text{m}$ , tooth length 83  $\mu\text{m}$ , and length of central plate 25  $\mu\text{m}$ . Morphology of the central plate was similar in all three locations (Fig. 14,  $y^1$ - $y^3$ ).

The differences in size among radulae and jaws and in morphology of the central plate seem too slight in the three locations to indicate species differences.

**Body shape.** Body shape is difficult to quantify in the highly contractible and extensible species of Prochaetodermatidae. The only measurements that are correlated to each other in all populations measured are posterium length to trunk length ( $P < .02$  to  $<.001$ ); other measurements such as trunk diameter to trunk length are not correlated at all, or are correlated in only some populations. Yet specimens with similar spicule morphology from different populations may appear to have a distinctive body shape, *e.g.*, short and stubby from 805 m in the North American Basin or long and slender 600 meters further downslope (Figs. 6, 7). Differences between mean values for the characters measured are statistically significant for some characters between some populations, but there is no consistent or clinal pattern (Table IV).

Therefore, to compare body shapes, an overall coefficient of similarity was determined for each of seven populations of *Prochaetoderma yongei*, identified as such by spicule morphology, and for comparison, for one population of *Spathoderma clenchi*, n. sp. (*q.v.*) which is very similar in shape but not in spicule morphology. The mean character difference (M.C.D.) was computed from five characters: trunk length, trunk diameter, posterium length, posterium diameter, and ratio of posterium length to trunk length (Table IV). Every population of *P. yongei* was compared with every other *P. yongei* population, a total of 21 comparisons; the *S. clenchi* population was compared with each of the 7 *P. yongei* populations. For each comparison between two populations, the absolute values of the differences between the five pairs of mean character values were summed and averaged, each mean character value having first been reduced by setting the maximum value for that character at 100.

The equation used for mean character difference by Sneath and Sokal (1973) is

$$\frac{1}{n} \sum_{i=1}^n |X_{ij} - X_{ik}|$$

where  $n$  = number of characters and  $X_{ij}$ ,  $X_{ik}$  = mean values of populations  $j$ ,  $k$  for character  $i$ . The lower the mean character difference is between two populations, the more similar they are.

The resulting six mean character differences (M.C.D.) for each population of *P. yongei* were summed to give an overall value (Table V, Total M.C.D.). A comparison of these summed M.C.D.'s indicates that the total for any one population is not strikingly different from that of any other, although the range in values are rather large. The highest value for summed M.C.D.'s (67.7) occurs at one end of the depth range,

TABLE IV

Mean value, standard deviation, and sample number for five characters in seven populations of *Prochaetoderma yongei* and one population of *Spathoderma clenchi*

Station and depth	Trunk length mm		Posterior length mm		Trunk diameter mm		Posterior diameter mm		Posterior length: Trunk length	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
	(n)		(n)		(n)		(n)		(n)	
<i>Prochaetoderma yongei</i>										
<i>No. American B.</i>										
CH-88 Sta. 207 805-811 m	1.11 (70)	.23	.36 (70)	.08	.37 (70)	.05	.22 (70)	.03	.33 (70)	.09
CH-50 Sta. 87 1102 m	1.38 (35)	.24	.48 (35)	.12	.34 (36)	.07	.19 (36)	.02	.35 (35)	.06
All-30 Sta. 128 1254 m	1.39 (44)	.23	.43 (44)	.08	.33 (42)	.05	.21 (44)	.03	.31 (44)	.04
All-12 Sta. 73 1470-1330 m	1.55 (137)	.27	.54 (137)	.11	.35 (136)	.06	.19 (133)	.03	.35 (137)	.06
CH-88 Sta. 209 1501-1693 m	1.16 (46)	.30	.38 (46)	.09	.31 (44)	.07	.21 (46)	.03	.34 (46)	.05
All-30 Sta. 131 2178 m	1.61 (15)	.25	.53 (15)	.17	.33 (15)	.07	.21 (15)	.04	.33 (15)	.08
<i>Namibia B.</i>										
All-42 Sta. 191 1600 m	1.39 (43)	.19	.41 (43)	.09	.38 (43)	.05	.22 (43)	.03	.30 (43)	.05
<i>Spathoderma clenchi</i>										
<i>No. American B.</i>										
All-30 Sta. 131 2178 m	1.01 (35)	.22	.51 (35)	.14	.35 (37)	.05	.22 (32)	.03	.51 (35)	.12

that is, in the population from the shallowest station; the lowest value (45.0) occurs in one of the populations at mid-depth range. The values for both total and range in M.C.D.'s in the population geographically most distant from the others (Namibia Basin) fall well within the values for other populations.

High total M.C.D. values, such as 67.7 for the short, stubby forms at the shallow station (Sta. 207) and 65.0 for the long, slender forms at the type locality at mid-depth range (Sta. 73), do not contain any taxonomic information on how these populations differ (Cain and Harrison, 1958); however, an examination of actual measurements (Table IV) indicates that in these two populations, differences in length are responsible for the high total M.C.D. values.

Body shape in specimens of *P. yongei* and *Spathoderma clenchi* is often so similar that species determination was always based on spicule morphology. However, the average M.C.D. value of the seven comparisons between the single *S. clenchi* population

TABLE V

Total, range and average mean character differences (M.C.D.'s) between seven populations of *Prochaetoderma yongei*, and range and average M.C.D.'s between one population of *Spathoderma clenchi* and the seven *P. yongei* populations

Station	Depth m	Total M.C.D.*	Range of M.C.D.'s	Average M.C.D.
<i>Prochaetoderma yongei</i>				
<i>No. American B.</i>				
CH-88 Sta. 207	805-811	67.7	5.8-16.7	11.3
CH-50 Sta. 87	1102	51.2	4.9-12.9	8.5
AI-30 Sta. 128	1254	45.0	4.7-10.5	7.5
AI-12 Sta. 73	1470-1330	65.0	4.8-16.7	10.8
CH-88 Sta. 209	1501-1693	60.7	5.8-15.1	10.1
AI-30 Sta. 131	2178	59.8	4.8-15.5	10.0
<i>Namibia B.</i>				
AI-42 Sta. 191	1600	56.3	4.7-13.1	9.4
<i>Spathoderma clenchi</i>				
<i>No. American B.</i>				
AI-30 Sta. 131	2178	**	14.9-19.7	17.2

\* See text for explanation.

\*\* Total M.C.D.'s between *S. clenchi* and *P. yongei* are meaningless.

and the seven *P. yongei* populations is 17.2, much higher than the average values—7.5 to 11.3—among *P. yongei* populations, although there is considerable overlap in the ranges of values in the two species. Thus mean character difference seems to be a sensitive measure of similarity in body shape within a species and of dissimilarity between two species.

The only character that is significantly different in all comparisons between the two species is the ratio of postterium length to trunk length (*t*-test of the means,  $P < .001$  for all populations), and it is this character difference which accounts for the high M.C.D. values in *S. clenchi*. In contrast, the shallowest population of *P. yongei* was not significantly different from any other population of *P. yongei* in mean postterium- to trunk-length ratio, although it is the population with the highest value for total M.C.D. and the appearance of being most different in body shape. On the other hand, this ratio is not a perfect species indicator, for among all 7 *P. yongei* populations it was significantly different in 5 out of the total 21 comparisons.

It is concluded that (1) there is not sufficient difference in body shape, as quantified by mean character difference, among populations of *P. yongei* to consider that any of them belong to a different species; and (2) the ratio of postterium length to trunk length is an important taxonomic character in species of Prochaetodermatidae.

#### Distribution

*Prochaetoderma yongei* is very widely distributed on the continental slope between 800 and 2000 m in the northwestern and eastern Atlantic (Table I; Fig. 1, solid circles). It does not occur in samples taken between Cape Hatteras and the Argentine Basin

in the western Atlantic or from depths less than 450 or greater than 2200 m. The samples in which it was taken in the eastern Atlantic are distributed at very great but rather even distances between 58°N and 23°S.

In the North American Basin, *P. yongei* is very abundant in both quantitative and nonquantitative samples; in the eastern Atlantic it is up to a hundredfold less abundant in sled trawls and was not taken in quantitative samples (Tables I, VII). Between depths of 1300 and 2100 m in both the northwestern and northeastern Atlantic *P. yongei* occurs sympatrically with the confamilial species *Spathoderma clenchi* (q.v.). In samples containing both species, *P. yongei* is the more abundant at depths less than 1800 m in the western Atlantic and 1900 m in the eastern Atlantic. (Anchor dredge samples are disregarded because of their inherent sampling bias.)

A single specimen of *P. yongei* taken from 530 m off Gay Head is 2.8 mm long, large for the species. A single specimen from 5042 m (CH-50 Sta. 81) is probably mislabeled.

#### *Specimens examined*

A total of 3122 specimens was examined, 2987 from the western Atlantic and 135 from the eastern Atlantic (Table I).

#### Genus *Spathoderma* n.g.

With characters of the family. Spicules spatulate, with flat base and relatively long, narrow blade rounded in cross-section, bent outward from body.

Distribution (based in part on species to be described): Atlantic continental slopes and abyssal plains.

From *spatha* (L.), a spatula.

Type species: *Spathoderma clenchi* n. sp., North American Basin.

#### *Spathoderma clenchi* n. sp.

Figs. 1, 3D-G, 4D, F, 9, 14 c<sup>1</sup>, c<sup>2</sup>; Tables I, III, IV, V, VII

*Prochaetoderma* sp. c. Scheltema, 1981, *Malacologia* 20: 363.

*Prochaetoderma* sp. A. Rowe, Polloni, and Haedrich, 1982, *Deep Sea Res.* 29: Table 2.

*Prochaetoderma* sp. A. Scheltema, 1985, in L. Laubier and C. Monniot, eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS, IFREMER, Brest*, pp. 391-396, Tables 1, 2, 3.

**Diagnosis:** Opaque, less than 2½ mm long, posterium ⅓ total length; oral-shield spicules indistinct; spicules bent slightly outwards and oriented parallel to long axis of body, without ornamentation, greatest length 232 µm, blades narrow with concave sides, bent sharply outwards, base with parallel sides; greatest jaw length 435 µm; greatest tooth length 100 µm; central radula plate long and relatively narrow, greatest length 45 µm.

This species is named in honor of Dr. William J. Clench, who first encouraged me to study mollusks.

**Holotype:** North American Basin, 39°38.5'N, 70°36.5'W, 2178 m (ATLANTIS II-30 Sta. 131, 18/XII/66). USNM No. 850209.

#### *Illustrated paratypes:*

Nos. 1, 2: Type locality. USNM Nos. 850210 (No. 1), 850211 (No. 2).

No. 3: West European Basin, 57°59.7'N, 10°39.8'W, 2091 m (INCAL DS-01, 15/VII/76). MNHN, Paris.

No. 4: West European Basin, 55°07.7'N, 12°52.6'W, 2897 m (INCAL DS-09, 20/VII/76). MNHN, Paris.

### Description

**External morphology.** *Spathoderma clenchi* is a small, opaque species with bent spicules which extend out from the body most noticeably at the junction of trunk and posteri-um; they are oriented parallel to the long axis of the body except ventrally, where they diverge along the midline (Fig. 3D-F). Average total body length at the type locality is 1.5 mm; greatest length is 2.2 mm. Both average and greatest trunk diameter are 0.4 mm. Posteri-um length is about 1/3 total length. Mean posteri-um length is 0.5 mm, and greatest length 0.9 mm; posteri-um diameter averages 0.2 mm and greatest diameter is 0.3 mm. The mean index of posteri-um to trunk length is 0.51, ranging from 0.27 to 0.87. The margin of the cloaca in lateral view is oblique. The oral shield is slightly larger than in *Prochaetoderma yongei* (Fig. 3G); oral shield spicules are present but not obvious.

Holotype: Total length 2.1 mm, trunk 1.4 mm by 0.4 mm, posteri-um 0.7 mm by 0.2 mm, index of posteri-um to trunk 0.50. Oral shield 0.06 by 0.12 mm; index of oral shield to trunk diameter 1.80.

**Spicules.** The spicules of *S. clenchi* lack ornamentation except for faint ridges on the blade seen only by scanning electron microscopy and an occasional subdued keel (Figs. 4D, F; 9). The sides of the base are straight and usually parallel; proximally the base is rounded or broadly triangular. In some spicules the base widens into a bulge at the waist. The sides of the blade are concave proximally at the waist where the blade rapidly narrows, except in spicules from region  $a_1$  and ventral region  $b_2$  where the blade may have convex sides.

The blade is narrow and sharply or roundly pointed. The isochromes are symmetrical. The thickest part of the spicule is at or just proximal to the waist in spicules from region  $b_1$ ; further posteriorly along the body, the thickest part is the blade. The width of the base is usually narrower in spicules from the posteri-um (region  $d$ ) than in those from the trunk. In lateral view the blade is bent sharply outwards, except in region  $a$  and in ventral region  $b_2$  where the blade is bent towards the body. Spicules from the ventral side of the body are smaller than those from the dorsal side. A few short, thin spicules with a short distal point are scattered on the body.

Ranges in dimensions of spicules from region  $c$  are given for four populations in three basins in Table III.

**Radula.** The jaws and teeth, examined in nine specimens, are large and typical for the family (Fig. 14  $c^1$ ,  $c^2$ ). Tooth length ranges up to 100  $\mu\text{m}$ , and jaw length and width up to 435 and 151  $\mu\text{m}$ , respectively. The radula has 8 to 10 rows of teeth. The central radula plate is curved and long, up to 45  $\mu\text{m}$ , and slender, up to 6  $\mu\text{m}$  wide, with the ends rounded or somewhat pointed.

### Distribution

*Spathoderma clenchi* has the same geographic range as *Prochaetoderma yongei*: from the northwestern to the northeastern Atlantic and south to the Namibia Basin in the eastern Atlantic; like *P. yongei* it is not found south of Cape Hatteras in the western Atlantic (Fig. 1, triangles). In vertical range, the two species overlap on the continental slope, but *S. clenchi* ranges deeper onto the abyssal rise, down to 3356 m

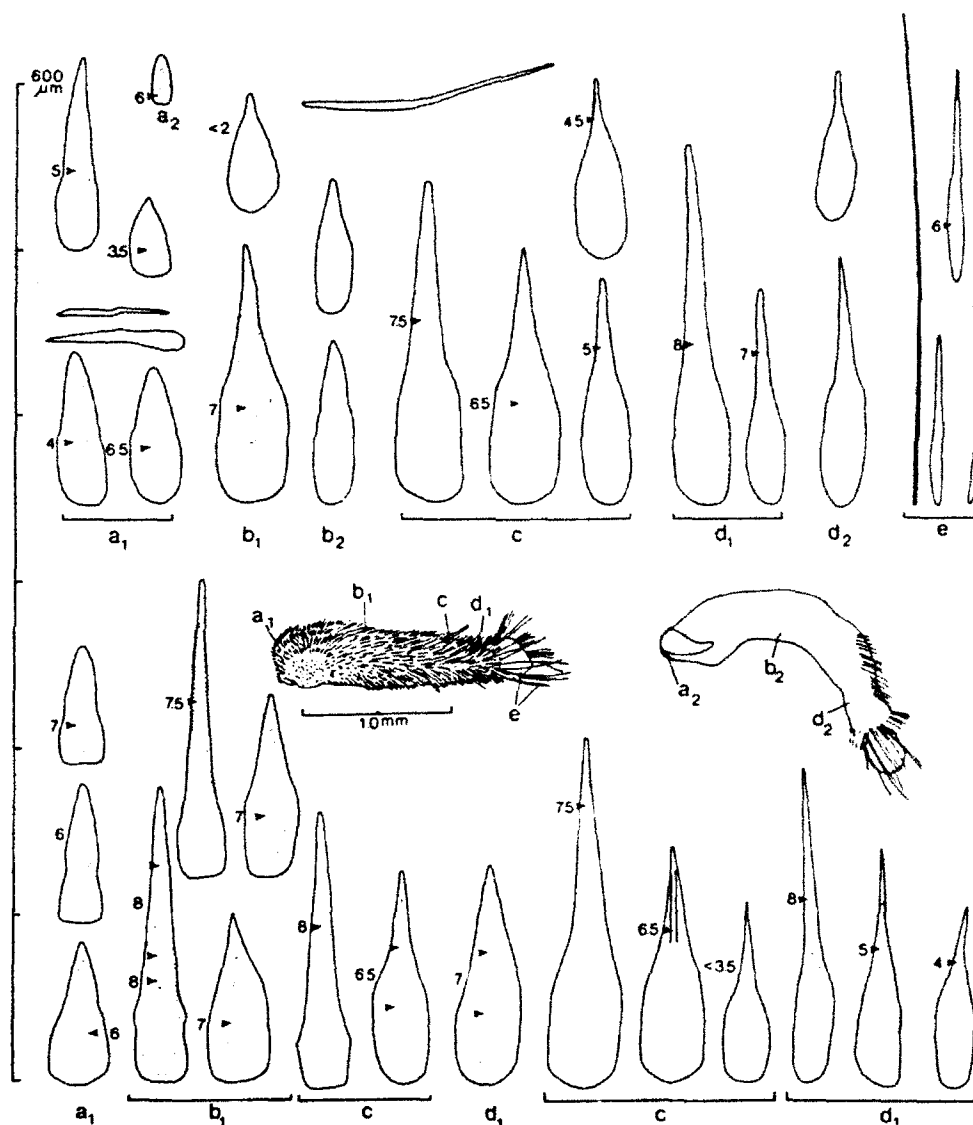


FIGURE 9. Spicules of *Spathoderma clenchi* n.g. n. sp. Upper row:  $a_1$ – $e$  from paratypes no. 1, left specimen, and no. 2, right specimen, 2178 m, North American Basin (type locality). Lower row:  $a_1$ – $d_1$  at left, spicules from several specimens from 1470 m, North American Basin (A II-12 Sta. 73);  $c$  and  $d_1$  at right, spicules from paratype no. 3, 2091 m, West European Basin (region  $d_1$  spicules somewhat oblique). Uppermost center spicule, lateral view showing blade (to right) bent outwards away from body; lateral views of  $a_1$  spicules, to left, are bent somewhat towards body.

(Table I). It is commonly found in samples taken at depths over 2000 m, and is sometimes abundant (Table VII).

#### *Specimens examined*

A total of 1480 specimens was examined, 682 specimens from the western Atlantic and 798 from the eastern Atlantic (Table I).

Genus *Chevroderma* n. g.

With characters of the family. Spicules asymmetrical, base of spicules long, with a longitudinal groove and regularly spaced, chevron-shaped cross grooves reflecting crossed fibers of cuticle (Fig. 5F). Spicules of trunk flat-lying and arranged obliquely, diverging on each side of ventral midline, spiralling up dorsally and posteriorly, and meeting at a slight or pronounced angle along dorsal midline (Fig. 3). Thickest part of spicule is dorsal to longitudinal groove, overlapping ventral, thin side of next adjacent spicule dorsal to it (Fig. 10, upper left).

Distribution: Lower continental slopes and abyssal plains of the Atlantic and Pacific; Aleutian Trench.

From *chevron* (Fr.), a chevron.

Type species: *Chevroderma turnerae* n. sp.

*Chevroderma turnerae* n. sp.

Figs. 1, 3 L-P, 5 B, D, F, 10, 15 L-P, Tables I, VI, VII

*Prochaetoderma* sp. C. Scheltema, 1985, in L. Laubier and C. Monniot eds., *Peuplements Profonds du Golfe de Gascogne. Campagnes BIOGAS, IFREMER, Brest*, pp. 391-396, Tables I, 2, 3.

**Diagnosis:** Large, opaque, up to  $5\frac{1}{2}$  mm in length and 0.8 mm in diameter, with a long posterium  $\frac{2}{5}$  or more total length; large oral shield and prominent oral shield spicules; spicules converge at pronounced angle along dorsal midline; trunk spicules up to 300  $\mu$ m with long base and wide, short blade bluntly pointed, thickened proximal to waist; radula and jaws large, teeth up to 140  $\mu$ m long, jaws up to 700  $\mu$ m long, and central plate long, up to 50  $\mu$ m, narrow, and curved.

This species is named in honor of Prof. Ruth D. Turner, who has given me many years of encouragement and advice.

**Holotype:** North American Basin, 35°50.0'N, 64°57.5'W, 4833 m (ATLANTIS II-24 Sta. 122, 21/VIII/66). USNM No. 850213.

**Illustrated paratypes:**

Nos. 1, 3: Type locality. USNM Nos. 850214 (No. 1), 850216 (No. 3).

No. 2: Angola Basin, 14°49'S, 9°56'E, 3797 m (ATLANTIS II-42 Sta. 195, 19/V/68). USNM No. 850217.

No. 4: Brazil Basin, 00°46.0'S, 29°28.0'W, 3459 m (ATLANTIS II-31 Sta. 156, 14/II/67). USNM No. 850219.

No. 5: West European Basin, 47°32'N, 9°35.9'W, 4237 m (BIOGAS-VI CP-14, 23/X/74). MNHN, Paris.

No. 6: Canary Basin, 27°14.9'N, 15°36.3'W, 2988 m (DISCOVERY 6711, 19/III/68). USNM No. 850221.

No. 7: Argentine Basin, 37°13.3'S, 52°45.0'W, 3305 m (ATLANTIS II-60 Sta. 259, 26/III/71). USNM No. 850223.

**Description**

**External morphology.** *Chevroderma turnerae* is large for a prochaetodermatid species with total body length averaging from 2.8 to 3.8 mm in three widely separated populations and ranging up to  $5\frac{1}{2}$  mm (Fig. 3L). Trunk diameter averages 0.5 mm, with greatest diameter 0.8 mm (Table VI). The posterium is long, from  $\frac{2}{5}$  to nearly

TABLE VI

Mean value, standard deviation, and sample number for five characters in four species of *Chevroderma* (*C. turnerae*, *C. gausson*, *C. scalpellum*, and *C. whitlatchi*)

Station and depth	Trunk length mm		Posterior length mm		Trunk diameter mm		Posterior diameter mm		Posterior length: Trunk length	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
	(n)		(n)		(n)		(n)		(n)	
<i>Chevroderma turnerae</i>										
<i>No. Amer. B.</i>										
All-24 Sta. 122 4833 m	1.9	.84	1.6	.68	0.5	.13	0.3	.09	.71	.20
	(11)		(10)		(11)		(11)		(10)	
<i>W. European B.</i>										
NOR. 113-EO13 4760 m	2.0	.72	1.6	.72	0.5	.13	0.3	.05	.80	.23
	(43)		(43)		(45)		(45)		(43)	
<i>Argentine B.</i>										
All-60 Sta. 245 (subsample) 2707 m	1.7	.50	1.1	.40	0.5	.12	0.3	.09	.69	.21
	(16)		(16)		(16)		(16)		(16)	
<i>C. gausson</i>										
<i>W. European B.</i>										
CH-106 Sta. 330 4632 m	1.7	.52	0.8	.21	0.6	.14	0.3	.07	.52	.12
	(8)		(8)		(8)		(8)		(8)	
<i>C. scalpellum</i>										
<i>Angola B.</i>										
All-42 Sta. 202 1427 m	1.0	.27	0.5	.15	0.4	.08	0.3	.05	.52	.12
	(50)		(50)		(50)		(50)		(50)	
<i>C. whitlatchi</i>										
<i>Aleutian Trench</i>										
SEVENTOW H-39 7298 m	1.0	.43	0.6	.36	0.3	.02	0.2	.06	.63	.14
	(31)		(31)		(31)		(31)		(31)	
<i>Panama B.</i>										
ALVIN dives 3912 m	0.9	.35	0.6	.19	0.3	.08	0.2	.05	.71	.26
	(31)		(31)		(31)		(31)		(31)	

1/2 body length; it averages 1.1 to 1.6 mm in length in three populations, with greatest length 2.9 mm, and 0.3 mm in diameter, with greatest diameter 0.5 mm. The posterior to trunk ratio averages 0.69 to 0.80, but the range is very large, from 0.32 to 1.36. The spicules of the trunk meet at a distinct angle along the dorsal midline (Fig. 3N).



The long spicule blades of the posterium extend out from the body. There are two rows of prominent oral shield spicules; the oral shield is distinctively large (Fig. 3O, P). The margin of the cloaca in lateral view is slanted.

Holotype: Total length 4.7 mm, trunk 2.8 by 0.7 mm; posterium 1.9 by 0.4 mm; index of posterium to trunk 0.68. Oral shield 0.14 by 0.17 mm; index of oral shield to trunk diameter 3.40.

*Spicules.* Trunk spicules are thick, with a long base relative to a short, wide blade that tapers to a rounded point (Figs. 5B, D, and 10, *b, c*). Greatest length is about 300  $\mu\text{m}$ . The base is slightly rotated about its long axis. Greatest thickness, up to 8.5  $\mu\text{m}$ , is about midway lengthwise, proximal to the waist. The sides of the base are somewhat convex, with the dorsal edge curved more than the ventral edge; the proximal end is rounded to somewhat pointed. The waist is either distinct or indistinct. The longitudinal groove usually runs the entire length of the base and often onto the blade. The blade is straight, or bent slightly outward. Spicules from the ventral side of the trunk are shorter but not narrower than spicules from the lateral and dorsal sides; the waist is not distinct (Fig. 10 *b*<sub>2</sub>, *c*<sub>2</sub>).

Oral shield spicules are large and thick (Fig. 10*a*<sub>2</sub>); spicules at the junction of anterium and trunk (*a*<sub>1</sub>) are thick and symmetrical. Spicules of the posterium (*d*) are more nearly symmetrical than those of the trunk; some are quite narrow and thickest at the waist, similar to spicules of *C. gaoson* n. sp. (*q.v.*). Trunk spicules of immature specimens are sharply pointed (Fig. 10B left).

Faint ridges occur on some or all of the trunk spicules in populations other than those from the North American Basin, which lack ridges. At least some spicules from the posterium are ridged in every population (ridges not illustrated).

*Radula:* The teeth and jaws from ten specimens were examined; they are large and typical for the family (Fig. 15 *t*<sup>1</sup>–*t*<sup>3</sup>). Teeth range up to 140  $\mu\text{m}$  in length; jaws range up to 700  $\mu\text{m}$  in length and 300  $\mu\text{m}$  in width, but are usually between 500 and 600  $\mu\text{m}$  in length and between 200 and 250  $\mu\text{m}$  in width. The central plate is long, to 50  $\mu\text{m}$ , relatively narrow, up to 10  $\mu\text{m}$ , curved, and tapered at the ends. The ash membrane and the wing may be thickened, or tanned, in distal teeth.

### *Morphological variation*

Greatest geographic variations in spicule morphology are in base width and degree of asymmetry. Spicules from specimens from the North American and deepest West European Basin have narrow bases relative to most other populations (Fig. 10, upper row and W spicules 1, 5). Wide-based spicules occur along with narrow-based spicules in the populations of the Brazil and Argentine Basins and the West European Basin (Fig. 10B, A, W spicules 3, 4). Spicules are all relatively wide-based from specimens taken from the Canary Basin southwards in the eastern Atlantic (Fig. 10C, An, N).

Most samples of *Chevroderma turnerae* are either too small for statistical analysis of body shape (see Table I) or comprised of mostly immature specimens. Samples from three widely separated geographic regions—North American Basin (ATLANTIS II-24 Sta. 122), West European Basin (NORATLANTE 113-E013), and Argentine Basin (ATLANTIS II-60 Sta. 245)—show no significant difference between means of five body measurements among the three populations except in posterium length (Table VI). In the Argentine Basin population, posterium length is statistically—and noticeably—shorter than in the other two populations. However, the ratio of posterium length to trunk length is not significantly different among the three populations.

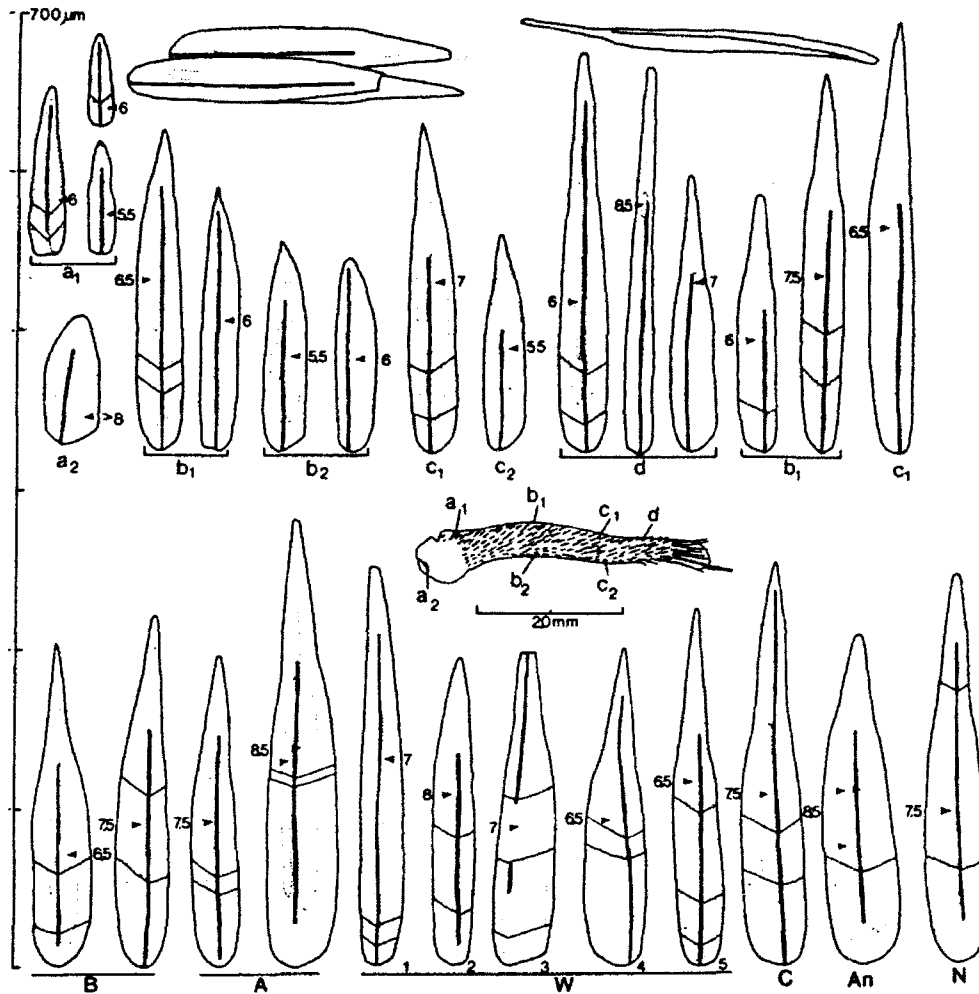


FIGURE 10. Spicules of *Chevroderma turnerae* n.g. n. sp. Upper row:  $a_1$ – $d$  at left, paratype no. 1 (figured specimen), and  $b_1$ ,  $c_1$  at right, paratype no. 3, 4833 m, North American Basin (type locality); upper left, overlapped spicules showing *in situ* arrangement, anterior end to left, dorsal side uppermost; upper right, lateral view showing rotation and outward bend of short blade. Lower row: variation in morphology of spicules from trunk regions  $b_1$  and  $c_1$ : B. immature specimen, paratype no. 4, 3459 m, Brazil Basin; A. two specimens from 3305 m, Argentine Basin, right spicule paratype no. 7; W. several specimens from West European Basin: spicule 1 from a deep station at 4823 m (INCAL CP-10), spicules 2 and 3 from shallower stations at 2897 and 2634 m (INCAL DS-09 and OS-01), spicules 4 and 5 from 4237 and 4706 m at stations further east in the Bay of Biscay (paratype no. 5 and BIOGAS VI CP-17); C. paratype no. 6, 2988 m, Canary Basin; An. paratype no. 2, 3797 m, Angola Basin; N. immature specimen, 4184 m, Namibia Basin (WALDA DS-04).

The larger size, but not the shape, of spicules also differentiates the shallower Argentine Basin population of *C. turnerae* from the other two populations (Fig. 10A).

Jaw length in one of two Argentine Basin specimens is great (700  $\mu$ m) compared to jaw length in five specimens from three other widely separated populations (493–580  $\mu$ m, North American, West European, and Angola Basins). However, jaw length

in the second Argentine Basin specimen (560  $\mu\text{m}$ ) falls within the limits measured in the other three populations.

On the bases of body measurements and spicule and radula morphology, the Argentine Basin continental slope populations of *C. turnerae* are considered to be small, short-tailed members of the species.

#### Distribution

*Chevroderma turnerae* is a cosmopolitan abyssal species of the Atlantic basins, absent only in samples from the Guyana and Iberian Basins (Table I; Fig. 1, open circles). Its depth range is also great, from a little over 2100 m to 5208 m. It is most commonly found at depths greater than 3000 m except in the Argentine Basin, where it was taken in largest numbers at depths less than 3000 m.

*Chevroderma turnerae* has never been taken in large numbers at any one locality, even with an epibenthic sled trawl; the greatest densities sampled quantitatively were in the Bay of Biscay (Tables I, VII).

#### Material examined

Five hundred thirty-eight specimens were examined, 222 from the western Atlantic and 316 from the eastern Atlantic.

#### *Chevroderma gauson* n. sp.

Figs. 1, 3Q-T, 5A, 11, 15 g<sup>1</sup>, g<sup>2</sup>; Tables I, VI

*Prochaetoderma* sp. D. Scheltema, 1985, in L. Laubier and C. Monniot, eds., *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS, IFREMER, Brest*, pp. 391-396, Tables 1, 2.

**Diagnosis:** Opaque, broad, with very long spicules distinctly bent outward from body; greatest body length 3.6 mm, greatest diameter 0.8 mm, posterium  $\frac{1}{3}$  total length and broad; oral shield spicules small, indistinct; trunk spicules up to nearly 500  $\mu\text{m}$ , thickest at distinct waist, blade long, narrow, and bent outwards, longitudinal groove distinct to faint; radula large, teeth up to about 130  $\mu\text{m}$  in length, jaws up to 626  $\mu\text{m}$ , central plate long, up to 48  $\mu\text{m}$ , wide and thick with a shallow groove, ends blunt.

The species name means "bent outwards."

**Holotype:** West European Basin, 50°43.5'N, 17°51.7'W, 4632 m (CHAIN-106 Sta. 330, 24/VIII/72). USNM No. 850226.

#### Illustrated paratypes:

No. 1: West European Basin, 50°04.7'N, 15°44.8'W, 4426 m (CHAIN-106 Sta. 328, 23/VIII/72). USNM No. 850229.

No. 2: Type locality. USNM. No. 850227.

No. 4: West European Basin, 48°19.2'N, 15°15.9'W, 4829 m (INCAL 0S-02, 2/VIII/76). MNHN, Paris.

No. 5: West European Basin, 48°19.2'N, 15°23.3'W, 4829 m (INCAL WS-03, 1/VIII/76). MNHN, Paris.

#### Description

**External morphology.** *Chevroderma gauson* is a moderately large, broad, opaque species with very long spicules which are bent outward and spiral upwards and pos-

TABLE VII

Vertical distribution, average sample number, and greatest density of three Prochaetodermatidae species in the North American and West European Basins

Depth m	Samples (N)*		Samples with species	No. Amer. B.			Samples with species	W. Europ. B.		
	No. Amer. B.	W. Europ. B.		No. individ. ( $\Sigma \bar{X}$ )	$\Sigma X/N = \bar{X}$	$s^2_{\bar{X}}$		No. individ. ( $\Sigma \bar{X}$ )	$\Sigma X/N = \bar{X}$	$s^2_{\bar{X}}$
<i>Prochaetoderma yongei</i>										
0-500	6	3	1	3	0.5	3.0	0	—	—	—
501-1000	2	6	2	167	83.5	163.0	0	—	—	—
1001-1500	3	4	3	1942	647.3	422.5	1	19	4.8	18.8
1501-2000	1	14	1	435	435.0	—	5	17	1.2	5.3
2001-2500	5	45	4	281	56.2	95.2	3	8	0.2	3.2
2501-3000	6	23	0	—	—	—	0	—	—	—
3001-3500	1	6	0	—	—	—	0	—	—	—
3501-4000	7	5	0	—	—	—	0	—	—	—
4001-4500	1	43	0	—	—	—	0	—	—	—
4501-5000	22	28	0	—	—	—	0	—	—	—
>5000	4	0	0	—	—	—	—	—	—	—
Greatest density sampled**:				400 m <sup>-2</sup>			n.d.			
<i>Spathoderma clenchi</i>										
0-500	6	3	0	—	—	—	0	—	—	—
501-1000	2	6	0	—	—	—	0	—	—	—
1001-1500	3	4	1	19	6.3	19.1	0	—	—	—
1501-2000	1	14	1	6	6.0	—	1	2	0.1	2.9
2001-2500	5	45	5	579	115.8	125.1	14	417	9.3	154.0
2501-3000	6	23	0	—	—	—	10	342	14.9	102.4
3001-3500	1	6	1	1	1.0	—	1	10	1.7	9.8
3501-4000	7	5	0	—	—	—	0	—	—	—
4001-4500	1	43	0	—	—	—	0	—	—	—
4501-5000	22	28	0	—	—	—	0	—	—	—
>5000	4	0	0	—	—	—	—	—	—	—
Greatest density sampled**:				275 m <sup>-2</sup>			8 m <sup>-2</sup>			
<i>Chevroderma turnerae</i>										
0-500	6	3	0	—	—	—	0	—	—	—
501-1000	2	6	0	—	—	—	0	—	—	—
1001-1500	3	4	0	—	—	—	0	—	—	—
1501-2000	1	14	0	—	—	—	0	—	—	—
2001-2500	5	45	0	—	—	—	1	1	0.0	—
2501-3000	6	23	0	—	—	—	4	4	0.2	—
3001-3500	1	6	1	1	1.0	—	2	12	2.0	4.8
3501-4000	7	5	3	14	2.0	3.3	2	13	2.6	8.8
4001-4500	1	43	1	14	14.0	—	23	108	2.5	8.8
4501-5000	22	28	7	59	2.7	8.4	16	63	2.3	3.3
>5000	4	0	1	2	0.5	2.0	—	—	—	—
Greatest density sampled**:				8 m <sup>-2</sup>			24 m <sup>-2</sup>			

<sup>a</sup> Sanders sled trawl, "Chalut à perche," Oban sled, and Wormley trawl.

<sup>ab</sup> Spade box corer, Birge-Ekman box corer.

teriorly in broken diagonals (Fig. 3Q). Mid-dorsally the spicules are arranged nearly parallel to the long axis of the body (Fig. 3S). Total body length averages 2.5 mm in one population; greatest length is 3.6 mm (Table VI). The broad trunk averages 0.6 mm and ranges up to 0.8 mm in diameter. The posterium is one-third total length, and broad, 0.3 mm average. Posterium length averages 0.8 mm, with posterium to trunk length index averaging 0.52 but ranging widely, from 0.38 to 1.14. The oral shield spicules are small and indistinct beside a medium-size oral shield (Fig. 3T).

Holotype: Total length 2.6 mm; trunk 1.6 by 0.7 mm; posterium 1.0 by 0.4 mm; index of posterium to trunk length 0.62. Oral shield 0.08 by 0.13 mm; index of oral shield to trunk diameter 1.49.

**Spicules.** Trunk spicules are very long and often narrow; a long, narrow blade tapers from a distinct waist to an acute or rounded apex (Figs. 5A, 11). The greatest thickness, up to 9  $\mu$ m, is at the waist. Sides of the base are nearly parallel or slightly convex; the proximal end is usually triangular. The distinct or faint longitudinal groove seldom runs onto the blade. The blade is bent outward. Faint ridges often run along the base parallel to the longitudinal groove. The greatest length of the trunk spicules is nearly 500  $\mu$ m. The trunk bears a few short, thin spicules with sharply pointed, short blades. Spicules from the ventral midline of the trunk are short, with a short blade and distinct waist (Fig. 11b<sub>2</sub>). Spicules from the posterium (d) are similar to those of the trunk. Oral shield spicules (a<sub>2</sub>) are similar to, but smaller than, those of

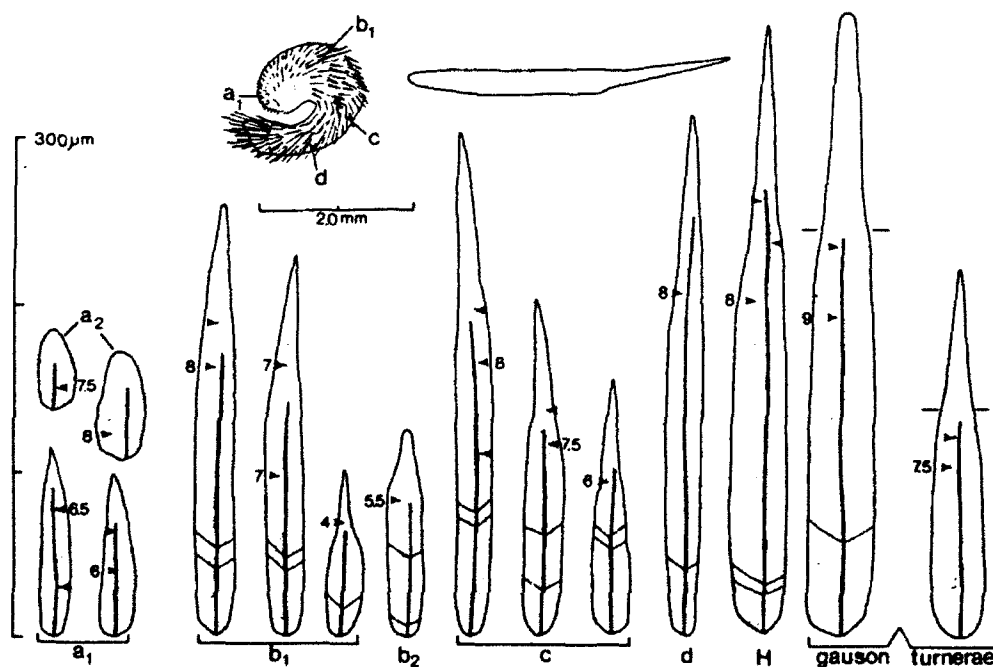


FIGURE 11. Spicules of *Chevroderma gauson* n. sp.: a<sub>1</sub>–d and specimen, paratype no. 1, 4426 m, West European Basin; oral shield spicules a<sub>2</sub> from paratype no. 2, 4632 m, West European Basin (type locality), and b<sub>2</sub> ventral trunk spicule from paratype no. 4, 4829 m, West European Basin; H, holotype, trunk spicule. Far right: spicules from specimens of *C. gauson* and *C. turnerae*, both of about average size, taken in the same sample at the type locality.

*C. turnerae*; spicules at the junction of anterium and trunk ( $a_1$ ) are similar in the two species.

**Radula.** The radula is typical for the family (Fig. 15  $g^1, g^2$ ). The teeth are probably large, up to perhaps 130  $\mu\text{m}$ ; however, exact measurements were not made because the tips of the posterior teeth from the three radulae examined were brittle and broke off in preparation, and the four anterior pairs of teeth were worn. The jaws are long, up to 626  $\mu\text{m}$ , and up to 261  $\mu\text{m}$  wide. The central plate is long, up 48  $\mu\text{m}$ , wide, up to 10  $\mu\text{m}$ , thick, and curved; it has a shallow groove running part or most of the length and the ends are blunt and rounded.

#### *Differentiation from C. turnerae*

*Chevroderma gauson* and *C. turnerae* were taken together in three out of the four stations where *C. gauson* occurred (Table I). Although the two species are distinctly different from each other in body shape where they co-occur, *C. gauson* is quite similar in shape to the short-tailed *C. turnerae* from the Argentine Basin continental slope and not significantly different from it in length or width of either trunk or posterium (Table VI). However, *C. gauson* is significantly different from all three *C. turnerae* populations analysed in the measure of posterium-to-trunk-length index ( $P < .05$ ).

Spicules of *C. gauson* and *C. turnerae* (Fig. 11, right) are distinguished primarily by length, relationship of greatest thickness to waist, and angle of blade to base, and secondarily by convexity of sides of the base, width of base and blade, shape of the proximal end, and distinctness of the waist. If they are visible in a specimen, the very large oral shield spicules of *C. turnerae* are distinctive.

The central plates distinguish the radulae of the two species (Fig. 15): in *C. turnerae*, but not *C. gauson*, the ends are tapered, and in *C. gauson*, but not *C. turnerae*, the plate is thick and bears a groove.

#### *Distribution*

*Chevroderma gauson* has been taken only at abyssal depths greater than 4400 m in the northern West European Basin north of 48°N (Table I; Fig. 1, squares). It was not taken in the abyss of the Iberian Basin just to the south (cruise ABYPLAINE, MNHN, Paris).

#### *Specimens examined*

The description is based on a total of 19 specimens from four stations.

#### *Chevroderma scalpellum* n. sp.

Figs. 1, 3U-W, 5C, 12, 15s; Tables I, VI

**Diagnosis:** Short, broad, translucent, less than 2½ mm long and up to 0.6 mm in diameter, posterium one-third total length; oral shield and oral shield spicules thin, small, and very indistinct; spicules with broad base, short, narrow blade, and distinct waist, with longitudinal groove not reaching proximal end of base, greatest length less than 300  $\mu\text{m}$ ; radula of moderate size, tooth length up to 106  $\mu\text{m}$ , jaw length up to 522  $\mu\text{m}$ , central plate long, 43  $\mu\text{m}$ , and narrow, 7  $\mu\text{m}$ , with blunt ends.

The species name means "a little scalpel."

**Holotype:** Angola Basin, 9°05'S, 12°17'E, 1427 m (ATLANTIS II-42 Sta. 202, 23/V/68). USNM No. 850231.

## Illustrated paratypes:

Nos. 1, 2: Type locality. USNM Nos. 850232 (No. 1), 850233 (No. 2).

No. 3: Cape Verde Basin, 10°30.0'N, 17°51.5'W, 1624 m (ATLANTIS II-31 Sta. 142, 5/II/67). USNM No. 850235.

## Description

**External morphology.** *Chevroderma scalpellum* is a very small, broad species averaging 1.5 mm in length and 0.4 mm in trunk diameter in one population (Table VI); the largest specimen is 2.4 mm long, and diameter ranges up to 0.6 mm. The posterium is broad, 0.3 mm on average, and one-third total body length, averaging 0.52 in posterium to trunk index; posterium length averages 0.5 mm and ranges from 0.3 to 0.8 mm. Mid-dorsally the spicules are arranged nearly parallel to the long axis of the body, but meet at a distinct angle where the trunk joins the posterium (Fig. 3W). The oral shield is small and indistinct with a thin cuticle; oral shield spicules are also small and indistinct (Fig. 3V).

**Holotype:** Total length 1.7 mm; trunk 1.2 by 0.5 mm; posterium 0.5 by 0.3 mm; index of posterium to trunk length 0.42. Oral shield 0.06 by 0.09 mm; index of oral shield to trunk diameter 1.08.

**Spicules.** The spicule base is broad relative to a usually short, narrow, often sharply pointed blade bent slightly outward; the waist is conspicuous (Figs. 5C, 12). Many spicules are nearly symmetrical. The longitudinal groove runs only part way along the base, not extending to the proximal edge but often extending onto the blade; it is sometimes nearly or totally lacking. The base may have faint, rather broad ridges and

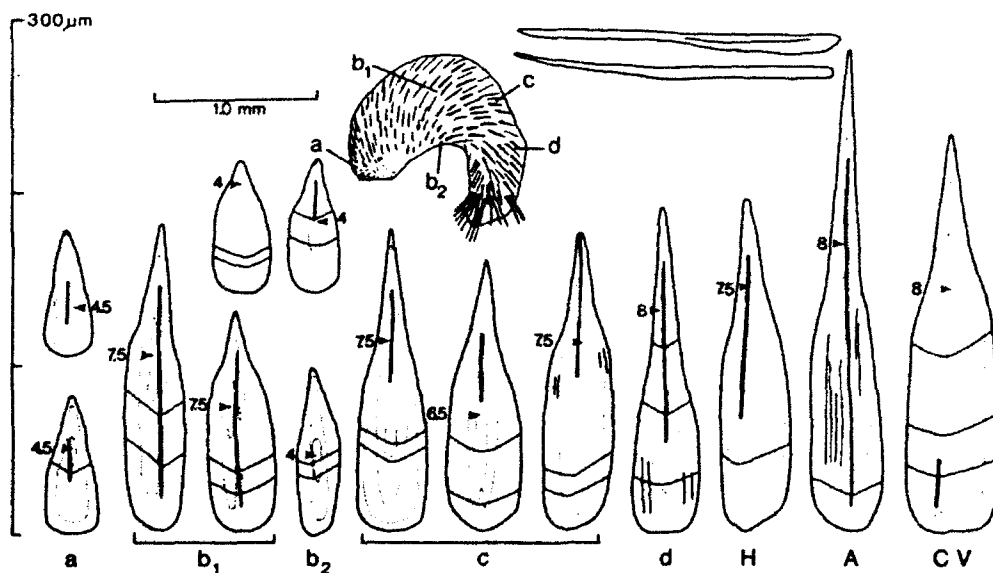


FIGURE 12. Spicules of *Chevroderma scalpellum* n. sp.: a-d and specimen, paratype no. 1, 1427 m, Angola Basin (type locality); H, holotype, trunk spicule; A, spicule from body region c of another specimen from type locality; CV, spicule from region c, paratype no. 3, 1624 m, Cape Verde Basin. Upper spicules: above, oblique view of body region c spicule; below, lateral view region d spicule; distal ends to left.

grooves; the sides of the base are straight to somewhat convex. Greatest thickness lies at the waist. Ventral spicules of the trunk (Fig. 12  $b_2$ ) are shorter than most other trunk spicules ( $b_1$ ) and are thickened further proximally. Spicules of the anterium ( $a$ ) have a broad base like those of the trunk. The bases of spicules from the posterium ( $d$ ) are the same length or shorter than those from the trunk, and the blades are bent further outward. Most spicules from trunk regions  $b$  and  $c$  of Angola Basin specimens are no longer than 225  $\mu\text{m}$ , but spicules from trunk region  $c$  in some specimens range up to nearly 300  $\mu\text{m}$  (Fig. 12A). Spicules from Cape Verde Basin specimens are larger, both broader and longer, than those from most of the Angola Basin specimens (Fig. 12CV).

*Radula.* The radula, examined from two specimens, is of moderate size for the family (Fig. 15s). Greatest tooth length is 106  $\mu\text{m}$ ; jaw length and width are up to 522 and 215  $\mu\text{m}$ , respectively. The central plate is long and narrow, up to 43  $\mu\text{m}$  long by 7  $\mu\text{m}$  wide, and has blunt, scarcely tapered ends.

*Differentiation from other Chevroderma species*

*Chevroderma scalpellum* is distinguished by its small size, indistinct oral shield, and spicules with their broad bases and short, narrow blades.

*Distribution*

*Chevroderma scalpellum* is an eastern Atlantic species found only in the Cape Verde and Angola Basins between about 10°N and 10°S over a narrow vertical range between 1427 and 2644 m (Table I; Fig. 1, hexagons).

*Specimens examined*

A total of 102 specimens from five samples was examined.

*Chevroderma whitlatchi* n. sp.

Figures 3H–K, 5E, 13, 15  $w^1$ ,  $w^2$ ; Tables II, VI

*Diagnosis.* Usually small, average length about 1.5 mm but up to 4.2 mm, with long posterium  $\frac{2}{5}$  total length; may have conspicuous translucent hump where trunk joins posterium; oral shield spicules small, distinct; spicules converge at angle along dorsal midline; trunk spicules with long base, distinct waist, and short, abruptly tapered, sharply pointed and broadly keeled blade, up to 200  $\mu\text{m}$  long; radula small, tooth with wing thickened and non-membranous, up to 100  $\mu\text{m}$  long, jaws up to 320  $\mu\text{m}$  long, central plate short with rounded ends.

This species is named for Dr. Robert B. Whitlatch, who gave me the Panama Basin material to examine.

*Holotype:* Panama Basin, 5°20.7'N, 81°56.2'W, 3912 m (ALVIN Dive 1239, Control 3, Core #2, 14/VI/82). USNM No. 850237.

*Illustrated paratypes:*

No. 1: Type locality (ALVIN 1232 Inj. BC #2). USNM No. 850238.

Nos. 2, 3: Aleutian Trench, 50°58.0'N, 171°37.5'W, 7298 m (SEVENTOW Leg 7, H-39, 20/VII/70). USNM Nos. 850240 (No. 2), 850241 (No. 3).



### Description

**External morphology.** *Chevroderma whitlatchi* is small and opaque; in many contracted specimens, the trunk is broadest posteriorly, producing a translucent hump at the juncture with the posterium. Spicules of the anterior half of the trunk, when it is contracted, assume an upright position; further posteriorly they meet at a distinct angle with the tips overlapped along the dorsal midline (Fig. 3H). They are arranged parallel to the body along the dorsal side of the posterium. Total length averages 1.5 and 1.6 mm in two populations (Table VI), with greatest length 4.2 mm. Trunk diameter averages 0.3 mm and ranges up to 0.6 mm. The posterium is long, two-fifths total length, and averages 0.6 mm in length by 0.2 mm in diameter, with greatest dimensions 2.1 and 0.3 mm, respectively; posterium to trunk length index averages 0.63 and 0.71 in the two populations, with a large range, 0.36 to 1.33. The two populations were not significantly different in any of five body measurements (Table VI). The oral shield spicules are small but distinct; the oral shield is large (Fig. 3K).

**Holotype:** Total length 2.7 mm; trunk 1.6 by 0.4 mm; posterium 1.1 by 0.3 mm; index of posterium to trunk 0.69. Oral shield 0.08 by 0.17 mm; index of oral shield to trunk diameter 3.0.

**Spicules.** The blade of trunk spicules is short relative to the base and narrow, abruptly tapering from a distinct waist to a usually pointed apex (Figs. 5E, 13c, H, A). The blade is bent outwards from the body wall and usually bears a medial ridge (juvenile) or distinct broad keel. The base is narrow and rotated about the long axis. The sides of the base are usually nearly straight and tapered proximally, so that the base is widest at the waist. Trunk spicules are thickest at, or just distal to, the waist. The longitudinal groove seldom extends beyond the base and may be very faint. Greatest spicule length is about 200  $\mu$ m. Spicules from the anterior trunk ( $a_1$ ) are wide; those from the ventral side of the trunk ( $b$ ) have a distinct waist. Spicules from the

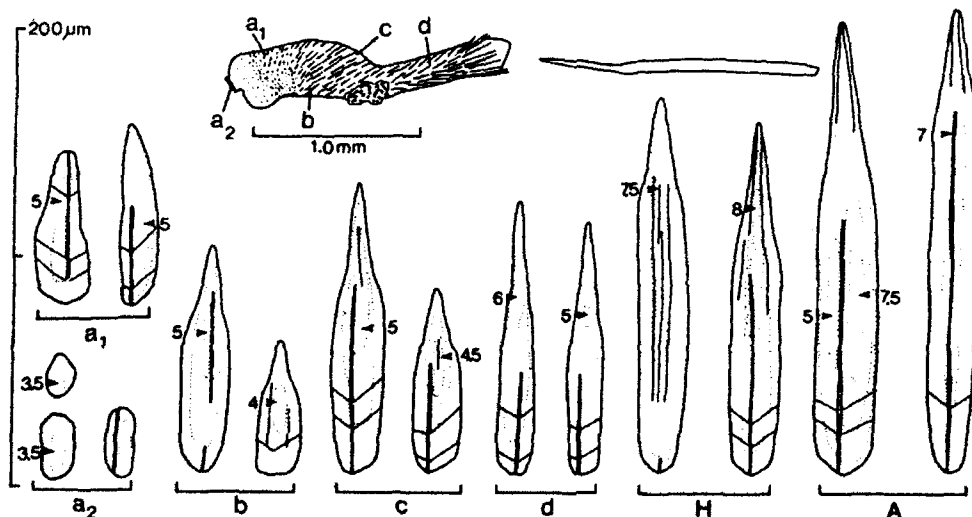


FIGURE 13. Spicules of *Chevroderma whitlatchi* n. sp.:  $a_1$ - $d$  and specimen, paratype no. 1, juvenile, 3912 m, Panama Basin (type locality); H, holotype, body region c; A, region c spicules from two specimens, 7298 m, Aleutian Trench, right spicule from paratype no. 3;  $a_1$  above, lateral view, distal end to left, showing outward bend of blade.

posterium ( $d$ ) have a narrower base and longer blade than those from the trunk. The oral shield spicules ( $a_2$ ) are small and thin.

**Radula.** The radula and jaws differ from other species of *Chevroderma* in their smaller size; in the thickened, twisted base of the jaws; in the serrations of the brush membrane, which are either very thin or lacking (although present in juvenile specimens); and in the thickened, non-membranous tooth wing (Fig. 15w<sup>1</sup>, w<sup>2</sup>). In four specimens examined, tooth length was 110  $\mu$ m in a large specimen 3.3 mm long and jaw length and width 429  $\mu$ m and 157  $\mu$ m, respectively; in specimens of average length, tooth length is about 70  $\mu$ m and jaw length and width range up to 320 and 110  $\mu$ m, respectively. The central plate is short, up to 27  $\mu$ m, and 5 to 7  $\mu$ m wide, with usually rounded, untapered ends.

#### Distribution

*Chevroderma whitlatchi* is an abyssal and hadal species taken in the central and eastern North Pacific. It occurs at high densities in the soupy muds of the Panama Basin and Aleutian Trench. Like *C. turnerae*, it covers a great depth range, from

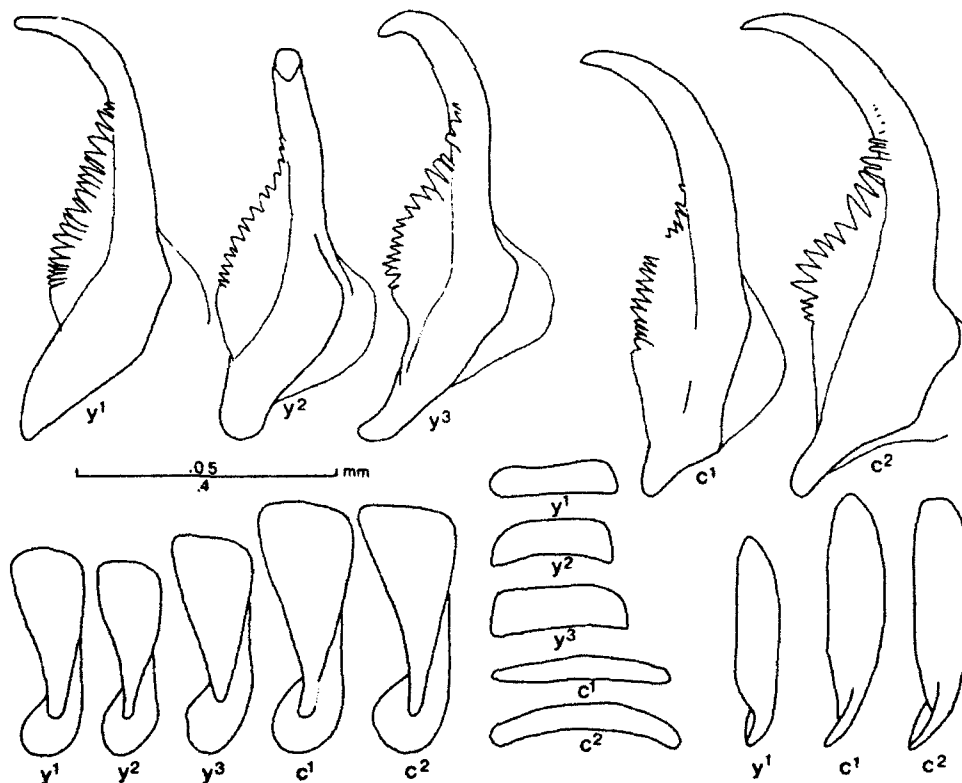


FIGURE 14. Radula teeth, central plates and jaws of *Prochaetoderma yongei* n. sp. and *Spathoderma clenchi* n.g. n. sp. y = *P. yongei*: y<sup>1</sup> paratype no. 1, 1470 m, North American Basin (type locality); y<sup>2</sup> paratype no. 3, 805 m, North American Basin; y<sup>3</sup> paratype no. 2, 1546 m, Namibia Basin; c = *S. clenchi*: c<sup>1</sup> paratype no. 2, 2178 m, North American Basin (type locality); c<sup>2</sup> paratype no. 4, 2897 m, West European Basin. Scale equals 0.05 mm for teeth and central plates and 0.4 mm for jaws.

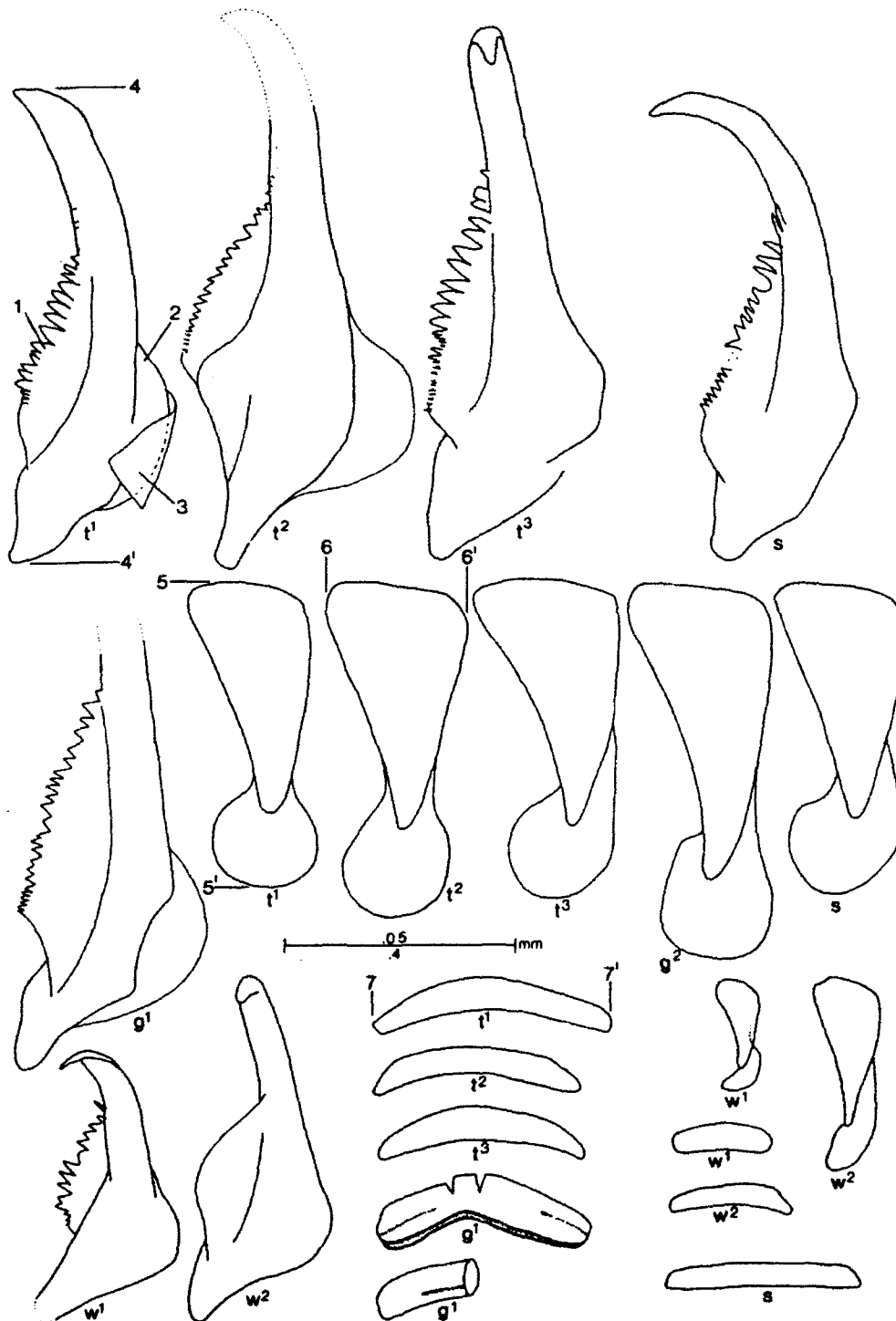


FIGURE 15. Radula teeth, central plates and jaws of *Chevroderma* (n.g.) species. t = *C. turnerae* n. sp.: t<sup>1</sup> paratype no. 3, 4833 m, North American Basin (type locality); t<sup>2</sup> specimen from 3305 m, Argentine Basin (All-60 Sta. 259); t<sup>3</sup> paratype no. 2, 3797 m, Angola Basin; s = *C. scalpellum* n. sp.: paratype no. 2,

2800 m off Oregon and 2727 m near the Galapagos Rift to over 5000 m in the mid-Pacific and over 7000 m in the Aleutian Trench.

About 90 percent of the specimens in box core samples from the Aleutian Trench and Panama Basin occurred within the upper 2 to 3 cm of sediment; the remaining 10 percent were below this level.

#### *Material examined*

Sixty-eight specimens were examined, 62 of them from the Panama Basin and Aleutian Trench, the remaining 6 scattered among 4 locations (Table II).

### DISCUSSION

#### *Taxonomic characters*

The dependence on spicule morphology for delimiting species and genera in the Prochaetodermatidae is based on ease of use, accessibility of the character, and biological considerations. Spicules and the cuticle in which they are embedded probably not only serve as a protective cover, but also—and perhaps primarily—as antagonists to muscle activity during locomotion. They also may adapt the animals to particular horizons within the sediment. Very small differences between species in body wall musculature, which would be very difficult to determine histologically, can be expected to be magnified in the morphology of the spicules. Body wall musculature, and thus spicule morphology, is considered to be a conservative character.

The body measurements of preserved, contracted specimens, although not descriptive of living animals, are related to the arrangement of internal organs and body wall musculature and allow for statistical analysis not readily possible with spicules, which vary greatly in size within a single specimen. As most identifications of deep-sea Aplacophora will be of preserved specimens, body measurements should be of continuing usefulness.

The variability in taxonomic characters described here and interpreted as belonging to single species may actually be due to the existence of sibling species living in different basins, but there is neither sufficient knowledge about the reproductive biology of these animals nor adequate samples on which to base judgements. It has seemed most sensible to treat apparently minor character differences between specimens from different ocean basins as variations within a species, rather than naming species according to their locality, *i.e.*, by ocean basins. A like situation in the protobranch family Malletiidae has recently been treated in a similar manner (Sanders and Allen, in press).

#### *Distribution*

*Geographic.* Vertical depth distribution and horizontal geographic range are directly related to one another in the Prochaetodermatidae. Three of the five Atlantic species described here—*Prochaetoderma yongei*, *Spathoderma clenchi*, and *Chevroderma turnerae*—have vertical depth ranges greater than 1500 m; all three are amphi-Atlantic

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1427 m, Angola Basin (type locality); g = *C. gausson* n. sp.: g<sup>1</sup> specimen from 4632 m, West European Basin (type locality); g<sup>2</sup> paratype no. 1, 4426 m, West European Basin; w = *C. whitlatchi*: w<sup>1</sup> paratype no. 1, 3912 m, Panama Basin (type locality); w<sup>2</sup> specimen from 7298 m, Aleutian Trench (SEVENTOW Leg 7 Sta. H-39). 1 membranous serrated brush, 2 membranous wing, 3 lateral toothlike projection of radula membrane, 4-4' tooth length, 5-5' jaw length, 6-6' jaw width, 7-7' central plate length. Scale = 0.05 mm for teeth and central plates, 0.4 mm for jaws.

and have been taken from four or more ocean basins (Fig. 1, Table I). One, *C. turnerae*, is an abyssal species; both *P. yonsei* and *S. clenchi* are continental slope species that do not extend into the abyss below 3300 m. *Chevroderma scalpellum* and *C. gausson* have both restricted depth ranges and geographic distributions; the former, with a depth range of 1217 m, is restricted to two adjacent ocean basins, and the latter, with a depth range of 403 m, occurs only in the northern West European Basin.

Such a correspondence in range of vertical and horizontal distribution is not unique to the Prochaetodermatidae and is considered to be at least in part due to mode of development and dispersal ability (R. Scheltema, 1972; Sanders, 1977). For an example, the protobranch bivalves are a molluscan group similar to the Aplacophora in development insofar as it is known for the two groups, either a lecithotrophic larva develops within a ciliated, cellular test or development is direct. A compilation from studies on 27 protobranch species in six families or subfamilies in the Atlantic (Allen and Sanders, 1973, 1982; Sanders and Allen, 1973, 1977, in press) shows that fourteen protobranch species have vertical depth ranges less than 1500 m; all but one of these are restricted to one or two ocean basins and to one side of the Atlantic. The remaining 13 species have depth ranges greater than 1500 m and are all amphi-Atlantic or occur in more than one ocean; but unlike the Prochaetodermatidae with large depth ranges, all 13 extend into the abyss below 3300 m.

R. Scheltema (1972, Table II) showed that two out of seven species of the protobranch genus *Nucula* in the northwest Atlantic were abyssal and had depth ranges greater than 1500 m, geographic ranges in three amphi-Atlantic basins, and lecithotrophic development. In one species, however, a lecithotrophic larval stage was related to a restricted depth range (less than 1000 m) and a geographic range of only two amphi-Atlantic basins, so factors other than mode of development determine distribution. A detailed study of reproduction and development in the species of Prochaetodermatidae described here has not yet been made.

Species with a dispersal ability are assumed to be better able to become widespread in the continuous abyss than on the continental slopes. However, both *P. yonsei* and *S. clenchi* are broadly distributed geographically despite their restriction to less than 2178 and 3356 m, respectively, although in the western Atlantic they do not breach the partial zoogeographic barrier at 34°N and are restricted to the North American Basin, probably because of slope currents (Cutler, 1975). The abyssal *C. turnerae*, on the other hand, is ubiquitous throughout Atlantic basins, apparently missing only in the Iberian and Guyana Basins, the latter faunally unique for many taxa. The Pacific Ocean species *C. whitlatchi*, like *C. turnerae*, has both a very large depth distribution, extending from 2727 m to hadal depths over 7000 m, and a broad geographic range (Table II). The question arises, Why is the other abyssal *Chevroderma* species, *C. gausson*, so restricted in range? Does it have a different dispersal ability, or ecological requirements met only by the northern West European Basin?

*Distribution within ocean basins.* Only a few data exist on local abundances within a basin, and only for the North American and West European Basins in the Atlantic. From grabs and box cores come quantitative data on density of species as number per square meter and their rank order. From sled trawls come data on total numbers of individuals by species or higher taxa and their percent composition and rank order. For the Pacific, there are data from one ¼-m<sup>2</sup> box core taken in the Aleutian Trench, two ¼-m<sup>2</sup> box cores from the mid-Pacific, and fifteen 225 cm<sup>2</sup> box cores in the Panama Basin. Based on either percent of total individuals or on density per square meter, the data show that particular species of Prochaetodermatidae are numerically an important part of the fauna at certain localities in the North American Basin and eastern Pacific, but not in the West European Basin or mid-Pacific.

In the North American Basin, species diversity in the Prochaetodermatidae is low, only three species, but numbers of individuals may be very high locally for two of them: up to  $400\text{ m}^{-2}$  for *Prochaetoderma yongei*, with  $200\text{ m}^{-2}$  not uncommon, and up to  $275\text{ m}^{-2}$  for *Spathoderma clenchi*, with over  $100\text{ m}^{-2}$  not uncommon (G. T. Rowe, unpub. data). Expressed either in numerical rank order or as a percent of total fauna, *P. yongei* ranks first at depths of about 1760 m at  $39^{\circ}46'N$ ,  $70^{\circ}37'W$  and constitutes more than 6 percent of the fauna [Grassle, 1977, Table 2, *Prochaetoderma* sp. (abundance recalculated here); see also Table I, this paper: OCEANUS-10 Sta. 367, 370]. In a sled trawl sample near the same location, 911 *P. yongei* formed 3.6 percent of the total fauna (Table I: ATLANTIS II-12 Sta. 73; Hessler and Sanders, 1967, Table 3). Similarly, at somewhat greater depths between 2351 and 2673 m, *S. clenchi* ranked third in species abundance and formed 5.4 percent of the fauna (Rowe *et al.*, 1982, Table 2, *Prochaetoderma* sp. A; data are lumped from samples taken at several localities).

In the West European Basin the Prochaetodermatidae are represented by at least eight species, including those from the North American Basin (Scheltema, 1985). Although the diversity is greater than in the North American Basin, the numerical abundance of two species is lower: *P. yongei*, for which quantitative data are lacking, was taken only occasionally in sled trawls in low numbers and comprised only 0.07 percent or less of all individuals; *S. clenchi* formed at the most only 0.2 percent of the fauna, and in the Bay of Biscay, greatest densities were low,  $8\text{ m}^{-2}$ .

*Chevroderma turnerae* occurred in low densities throughout its range, with not more than 75 individuals taken in a single sled trawl and densities ranging from  $8\text{ m}^{-2}$  in the North Atlantic Basin to  $24\text{ m}^{-2}$  in the Bay of Biscay (Table I: OCEANUS-10 Sta. 353; BIOGAS XI KG-207).

Data from nonquantitative sled trawls for *P. yongei*, *S. clenchi*, and *C. turnerae* show similar vertical distribution patterns within the two north Atlantic basins, but, like data from quantitative gear, uneven abundances in the two slopes species. The number of sled trawl samples from all cruises are given for each basin by 500 m depth intervals in Table VII (N) (All western Atlantic samples were taken with a Sanders sled trawl; data for the West European Basin are based on samples from four types of sleds and trawls. Replicates taken on CENTOB cruises BIOGAS VI and INCAL sampled the aplacophoran fauna equally efficiently.) For each species, the number of samples in which it occurred at each depth zone was tabulated and the individuals in these samples summed ( $\Sigma X$ ; data from Table I). From these data the average number of individuals per sample was computed for each 500 m interval ( $\bar{X} = \Sigma X/N$ ).

All three species are most numerous in their mid-ranges, *P. yongei* and *S. clenchi* most markedly so in the North American Basin, where these two species are not only abundant, but also common, occurring in most trawl samples taken at their mid-ranges. The same species are less commonly found in the West European Basin, where they occurred in fewer than one-half the samples at all depths, and less abundant in individual samples, with 10 to one hundred-fold fewer individuals per sample. *Chevroderma turnerae* has low mean numbers of individuals per sample but is more evenly distributed across the ocean than either *P. yongei* or *S. clenchi*, occurring in about one-third of all samples in both basins.

The high variance-to-mean ratios ( $s_x^2/\bar{X}$ ) indicate a patchy distribution in both basins for all three species, as indicated also by the absolute sample sizes in Table I.

The Pacific species *C. whitlatchi* is very abundant in both the Panama Basin, where it ranges up to  $178\text{ m}^{-2}$ , and in the Aleutian Trench, with  $124\text{ m}^{-2}$ ; at the latter location it ranked second in species abundance (Jumars and Hessler, 1976; Hessler, unpub.). In four other localities, however, total numbers taken were only 1 or 2.

*Importance of Aplacophora in the deep sea fauna*

The Aplacophora are usually considered an insignificant part of the faunas in which they are found. Certainly the class is small in species numbers compared to other higher taxa in the deep-sea, *i.e.*, polychaetes, bivalves, crustaceans, and nematodes. It is, however, the individuals of species that interact, and certain species of Aplacophora therefore may have an important role in a community. Although the total polychaetes or bivalves present at a particular locality may outnumber the Aplacophora, a single aplacophoran species (*e.g.*, *Prochaetoderma yongei* or *Chevroderma whitlatchi*) nonetheless may be among the most abundant species present. The Prochaetodermatidae are thought to be omnivores that feed on a wide variety of organic material, probably living and dead (Scheltema, 1981), a feeding habit that equips them well, and perhaps better than most other species, to live in an environment where food may be limiting.

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## LITERATURE CITED

- ALLEN, J. A., AND H. L. SANDERS. 1973. Studies on deep-sea Protobranchia (Bivalvia); the families Siliculidae and Lametilidae. *Bull. Mus. Comp. Zool.* 145(6): 263-310.
- ALLEN, J. A., AND H. L. SANDERS. 1982. Studies on the deep sea Protobranchia: the subfamily Spinuliniae (family Nuculanidae). *Bull. Mus. Comp. Zool.* 150(1): 1-30.
- BOSS, K. J. 1982. Mollusca: Caudoloveata. Pp. 945-948 in S. P. Parker, ed. *Synopsis and Classification of Living Organisms*, vol. 1, McGraw Hill, NY.
- CAIN, A. J., AND G. A. HARRISON. 1958. An analysis of the taxonomists judgement of affinity. *Proc. Zool. Soc. Lond.* 131: 85-98.

- CUTLER, E. B. 1975. Zoogeographical barrier on the continental slope off Cape Lookout, North Carolina. *Deep Sea Res.* 22: 893-901.
- GRASSLE, J. F. 1977. Slow recolonisation of deep-sea sediment. *Nature* 265: 618-619.
- HESSLER, R. R., AND H. L. SANDERS. 1967. Faunal diversity in the deep sea. *Deep Sea Res.* 14: 65-78.
- JUMARS, P. A., AND R. R. HESSLER. 1976. Hadal community structure: implications from the Aleutian Trench. *J. Mar. Res.* 34: 547-560.
- KOWALEVSKY, A. 1901. Sur le genre *Chaetoderma*. *Arch. Zool. Exp., Ser. 3* 9: 264-274.
- ROWE, G. T., P. T. POLLONI, AND R. L. HAEDRICH. 1982. The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. *Deep Sea Res.* 29: 257-278.
- SALVINI-PLAWEN, L. v. 1969. Solenogastres und Caudofoveata (Mollusca, Aculifera): Organisation und phylogenetische Bedeutung. *Malacologia* 9: 191-216.
- SALVINI-PLAWEN, L. v. 1972. Die Caudofoveata des Mittelmeeres und das Genus *Scutopus* (Mollusca, Aculifera). Pp. 27-51 in *Fifth European Marine Biology Symposium*, B. Battaglia, ed. Piccin Editore, Padova.
- SANDERS, H. L. 1977. Evolutionary ecology and the deep-sea benthos. *Acad. Nat. Sci. (Philadelphia), Spec. Pub.* 12: 223-243.
- SANDERS, H. L., AND J. A. ALLEN. 1973. Studies on deep-sea Protobranchia (Bivalvia); prologue and the Pristiglomidae. *Bull. Mus. Comp. Zool.* 145(5): 237-262.
- SANDERS, H. L., AND J. A. ALLEN. 1977. Studies on deep-sea Protobranchia (Bivalvia); the family Tindariidae and the genus *Pseudotindaria*. *Bull. Mus. Comp. Zool.* 148(2): 23-59.
- SANDERS, H. L., AND J. A. ALLEN. In press. Studies on the deep-sea Protobranchia (Bivalvia); the family Mallettiidae. *Bull. Br. Mus. Nat. Hist. Zool.*
- SANDERS, H. L., R. R. HESSLER, AND G. R. HAMPSON. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep Sea Res.* 12: 845-867.
- SCHELTEMA, A. H. 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Z. Morphol. Tiere* 72: 361-370.
- SCHELTEMA, A. H. 1976. Two new species of *Chaetoderma* from off west Africa (Aplacophora, Chaetodermatidae). *J. Moll. Stud.* 42: 223-234.
- SCHELTEMA, A. H. 1978. Position of the class Aplacophora in the phylum Mollusca. *Malacologia* 17: 99-109.
- SCHELTEMA, A. H. 1981. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia* 20: 361-383.
- SCHELTEMA, A. H. 1985. The genus *Prochaetoderma* (Aplacophora, Mollusca) in the Bay of Biscay: initial account. Pp. 391-396 in *Peuplements Profonds du Golfe de Gascogne: Campagnes BIOGAS*, L. Laubier and C. Monniot, eds. IFREMER, Brest.
- SCHELTEMA, R. 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates: a speculative summary. Pp. 58-66 in *Barobiology and the Experimental Biology of the Deep Sea*, R. W. Brauer, ed. University of North Carolina Sea Grant Program, Chapel Hill.
- SCHWABL, M. 1963. Solenogaster mollusks from southern California. *Pac. Sci.* 17: 261-281.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. *Numerical Taxonomy*. W. H. Freeman & Co., San Francisco. xv + 573 pp.
- TREECE, G. D. 1979. Four new records of aplacophorous mollusks from the Gulf of Mexico. *Bull. Mar. Sci.* 29: 344-364.



COMPARATIVE MORPHOLOGY OF THE RADULAE AND ALIMENTARY TRACTS  
IN THE APLACOPHORA<sup>1</sup>

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## ABSTRACT

The alimentary tract was studied in one genus of Neomeniomorpha and in five genera of Chaetodermomorpha.

The cuticular oral shield of the Chaetodermomorpha is part of the foregut cuticle.

A dorsal ciliated tract or typhlosole, an unarticulated radula on a radular membrane, an odontophore with bolsters within the haemocoel, and paired tubular salivary glands are conservative molluscan characters. It is not certain whether an undivided stomach-digestive gland (Neomeniomorpha) or separate stomach and digestive diverticulum (Chaetodermomorpha) represents the primitive midgut in the Aplacophora. The molluscan style may primitively have been formed throughout the stomach and anterior intestine (*Scutopus*). A style sac with protostyle and a gastric shield have evolved together independently in one family of carnivorous Aplacophora (Chaetodermatidae).

The genera studied here exhibit an evolution of the radula from rows of distichous teeth firmly affixed to a divided or fused radular membrane to (1) a gastropod-like articulated radula and (2) a highly specialized pincers-like radula. The odontophore has evolved from a structure scarcely protruded into the buccal cavity to one with the tip lying free, surrounded by deep buccal pouches and sublingual cavity. A carnivorous diet is related both to a primitive radula (*Gymnomenia*) and to the specialized radulae of *Prochaetoderma* and the Chaetodermatidae (*Chaetoderma* and *Falcidens*).

Evolution to a gastropod-like radula combined with jaws which hold the mouth open in *Prochaetoderma* has made possible a diet which is independent of particle size. A broad food source may be one reason that some species of *Prochaetoderma* are numerically dominant members of the fauna in the deep sea, where food may be limiting.

## INTRODUCTION

The alimentary tract of the Aplacophora, excepting the radula, has generally received less attention than other organ systems. The radula itself has usually been described from histologic preparations; isolated radulae with complete radular membranes have been figured for only a few species in the subclass Chaetodermomorpha (= Caudofoveata) (Kowalevsky, 1901; Scheltema, 1972, 1976; Ivanov, 1979) and for only two species of *Epimenia* in the subclass Neomeniomorpha (= Solenogastres *sensu* Salvini-Plawen) (Baba, 1939, 1940). Gut morphologies have usually been described as part of species descriptions; no integrated overview exists for the class as a whole outside of literature reviews in the standard invertebrate treatises. The literature on feeding and digestion in the

Neomeniomorpha was reviewed by Salvini-Plawen (1967b), who has recently proposed evolutionary sequences in the digestive system in the mollusks (1980). The only developmental studies on the alimentary tract are for *Epimenia verrucosa* (Baba, 1938) and *Neomenia carinata* (Thompson, 1960).

This paper examines the morphologies of the radula and fore- and mid-guts of certain aplacophoran families and relates these morphologies to the feeding type and the ecologic importance of these families in the deep-sea benthos. Possible phylogenetic relationships of the aplacophoran radula and gut morphologies are proposed and the bearing of these relationships to understanding molluscan evolution is discussed. Primary consideration is given to the Chaetodermomorpha, but one primitive neomeniomorph is examined (Fig. 1).

<sup>1</sup>Contribution No. 4655 from the Woods Hole Oceanographic Institution.

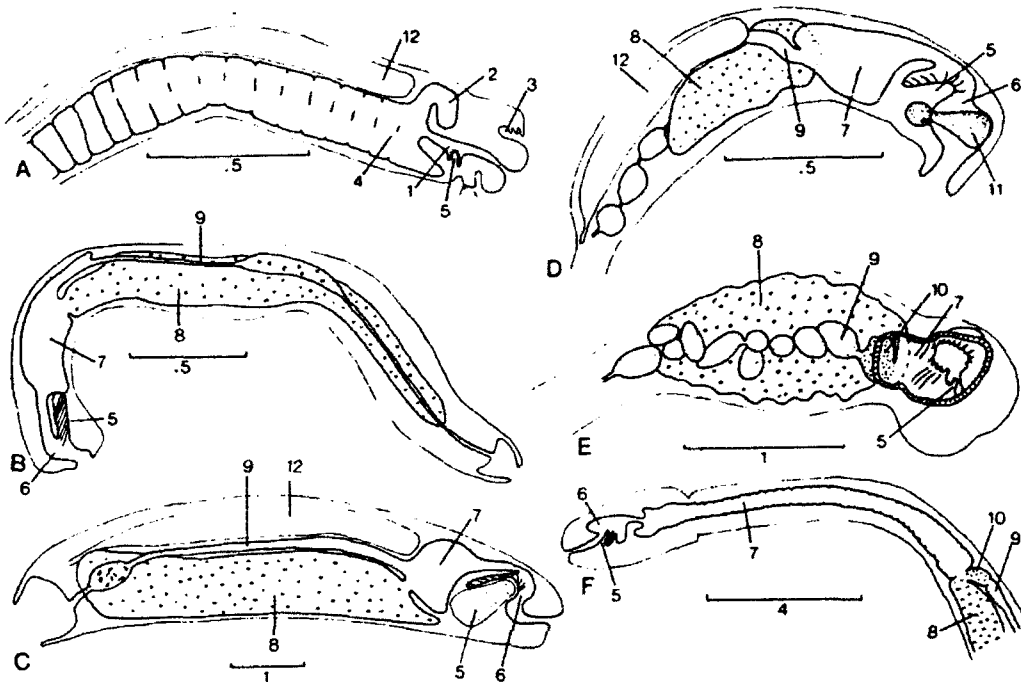


FIG. 1. Alimentary tract of Aplacophora, semi-schematic. A: *Gymnomenia* n. sp., anterior two-thirds only; B: *Scutopus robustus*; C: *Limifossor talpoideus*; D: *Prochaetoderma* sp. y, posterior end not shown; E: *Falcidens caudatus*, posterior end not shown; F: *Chaetoderma nitidulum*, anterior half only. A, F from sagittal sections; B-E from cleared specimens. Gonad not indicated in B, E, or F. Scales in mm. 1, foregut; 2, dorsal caecum; 3, atrium; 4, midgut of undifferentiated stomach and digestive gland; 5, odontophore and radula; 6, buccal cavity; 7, stomach; 8, digestive diverticulum; 9, intestine; 10, style sac; 11, jaws; 12, gonad.

#### MATERIALS AND METHODS

Thirteen species in four families and six genera were examined, two species by histologic sections only, three by isolated radula preparations only, and eight by both histologic and radula preparations. All unnamed species or species identified by letter only will be formally described elsewhere.

##### Subclass Neomeniomorpha

Fam. Wireniidae (regarded as primitive on basis of spicule shape, thin integument, and lack of ventral foregut glands, Salvini-Plawen, 1978).

(1) *Gymnomenia* n. sp. 620 m, off Walvis Bay, Namibia, Africa (23°00'S, 12°58'E). 4 specimens (cross and sagittal sections, 2 radula preparations).

##### Subclass Chaetodermomorpha

Fam. Limifossoridae (regarded as primitive on basis of vestige of ventral foot furrow in *Scutopus*, Salvini-Plawen, 1972a).

(2) *Scutopus megaradulatus* Salvini-Plawen, 1972. 650 m, off Cape Hatteras, North Carolina, U.S.A. (34°14.8'N, 75°46.7'W); 2 specimens (cross sections and radula preparation).

(3) *Scutopus robustus* Salvini-Plawen, 1970. 660 m, Bay of Biscay (48°56'N, 11°02'W); 4 specimens (sagittal sections, 2 gut dissections, and 1 radula preparation).

(4) *Limifossor talpoideus* Heath, T904. 508-572 m, Alaska; 3 specimens (type material) (cross and sagittal sections, whole mount).

(5) *Limifossor* n. sp. 188-195 m, off east Florida, U.S.A. (27°25'N, 79°53'W); 3 specimens (cross sections, 2 radula preparations).

cuticle itself appears to be homogeneous except for a thickened outermost layer of the oral shield and a zone of fibrils running between the epithelial cells of the oral shield and the cuticle (Fig. 2A, 7; C). The epithelial

cells of the oral shield contain vacuoles and secretory granules (Fig. 2A, F). In *Scutopus* the cuticle is pierced by channels and by scattered pyriform mucous cells which are not grouped into lobes (Fig. 2A). In *Chaetoderma*

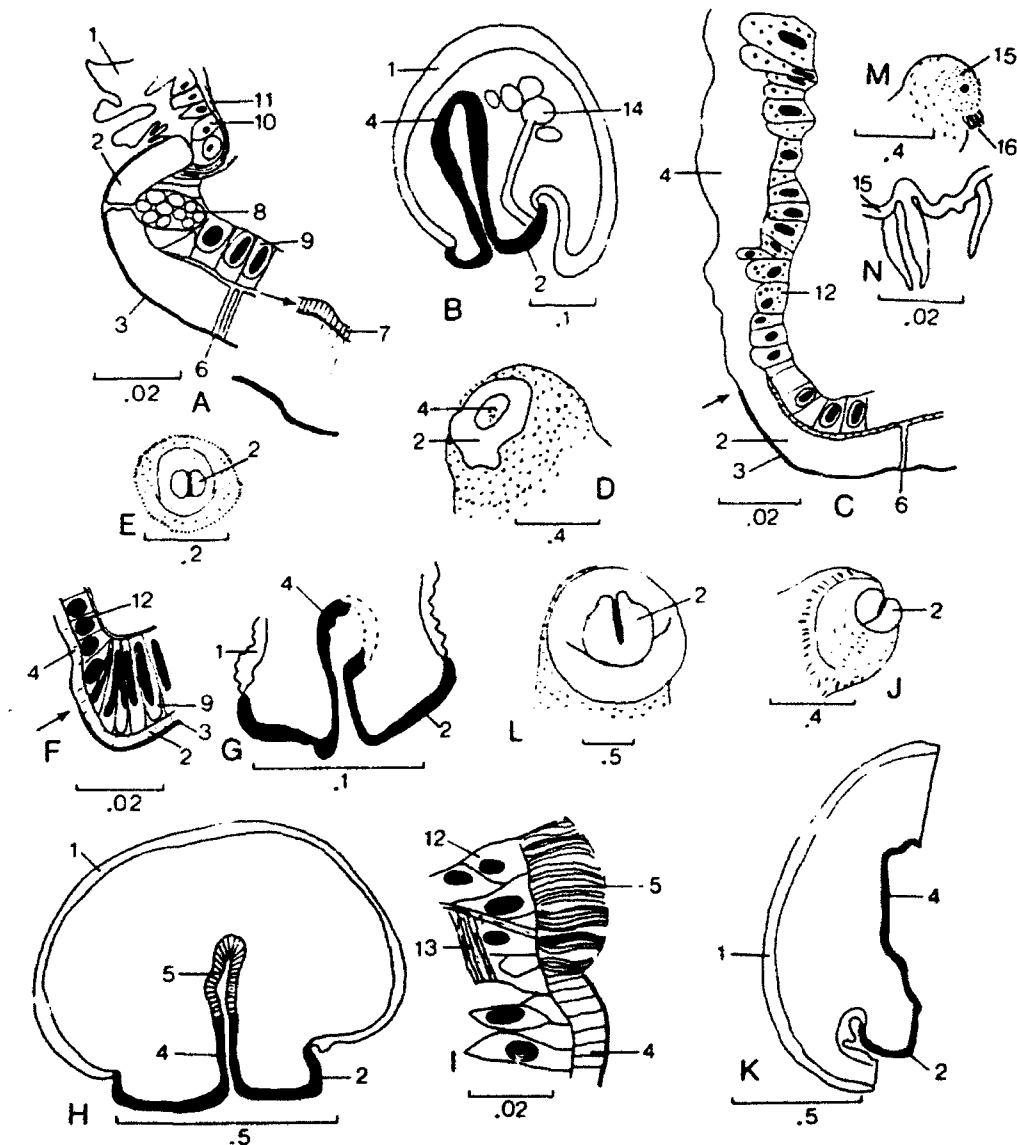


FIG. 2. Mouth of Aplacophora. A-D: *Scutopus megaradulatus*; E-G: *Prochaetoderma* sp. y; H, I, L: *Chaetoderma nitidulum*; J: *Limitosor* n. sp.; K: *Limitosor talpoideus*, one half of section; M, N: *Gymnomenia* n. sp.; B, G, H, K, cross-section through oral shield and oral tube, cuticle of gut black, cuticle of integument stippled; D, E, J, L, M, external views of mouth; A, detail of oral shield and integument; C, F, histologic detail of change from oral shield to oral tube (arrow); I, histologic detail of oral tube; N, tactile extensions of peri-oral cuticle. Scales in mm. 1, epidermal cuticle; 2, oral shield cuticle; 3, outer thickened layer of oral shield cuticle; 4, cuticle of oral tube; 5, cilia of oral tube; 6, channel; 7, zone of fibrils; 8, mucous cell; 9, vacuole; 10, epidermal cell; 11, muscle of body wall; 12, epithelial cell of oral tube; 13, muscles; 14, precerebral ganglion; 15, cuticular peri-oral fold; 16, cilia of pedal pit.

(6) *Limifossor ?fratula* Heath, 1911. Location unknown. 1 specimen (sagittal sections; Heath material).

#### Fam. Prochaetodermatidae

(7) *Prochaetoderma* sp. y. (a) 805–811 m, S of Woods Hole, Massachusetts, U.S.A. (39°51.3'N, 70°54.3'W); 6 specimens (radula preparations). (b) 1330–1470 m, S of Woods Hole (39°46.5'N, 70°43.3'W); 21 specimens (9 cross and sagittal sections, 12 radula preparations). (c) 1546–1559 m, off Walvis Bay, Namibia, Africa (23°05'S, 12°31'E); 1 specimen (radula preparation).

(8) *Prochaetoderma* sp. c. (a) 1330–1470 m, S of Woods Hole (39°46.5'N, 70°43.3'W); 4 specimens (radula preparations). (b) 2178 m, S of Woods Hole (39°38.5'N, 70°36.5'W); 2 specimens (radula preparations). (c) 2091 m, off Scotland (57°59.7'N, 10°39.8'W); 1 specimen (radula preparation).

(9) *Prochaetoderma* sp. p. 1624–1796 m, off Dakar, West Africa (10°30.0'N, 17°51.5'W); 6 specimens (2 cross and sagittal sections, 4 radula preparations).

#### Fam. Chaetodermatidae

(10) *Falcidens* n. sp. 650 m, off Cape Hatteras (34°14.8'N, 75°46.7'W); 1 specimen (radula preparation).

(11) *Falcidens caudatus* (Heath, 1911). 1102 m, S of Woods Hole (39°48.7'N, 70°40.8'W) and 1330–1470 m, S of Woods Hole (39°46.5'N, 70°43.3'W); 5 specimens (sagittal and cross sections).

(12) *Chaetoderma nitidulum* Lovén, 1844 (= *C. canadense* Nierstrasz, 1902; Scheltema, 1973). 74 m, St. Margaret's Bay, Nova Scotia (44°33'01"N, 65°58'09"W). 4 specimens (sagittal and cross sections) and numerous radula preparations.

(13) *Chaetoderma abidjanense* Scheltema, 1976. 80 m, off Ivory Coast, West Africa (5°02.5'N, 3°47'W); 1 specimen (radula, redrawn from Scheltema, 1976).

Most specimens were fixed as part of an entire washed sample in 10% buffered formalin and changed for preservation to 70 or 80% ethyl alcohol within 24 hr. *Chaetoderma nitidulum* was fixed in Bouin's for histologic sections; all others were refixed in HgCl<sub>2</sub> and acetic acid before sectioning. Stains employed were Delafields' haematoxylin, with eosin, Gray's double contrast, or Ponceau S

as counter-stains. Radulae were isolated by dissecting out the buccal mass and treating with 5% sodium hypochlorite (household bleach) to remove the tissue. The isolated radulae were washed in distilled water and examined in glycerin using a Zeiss interference contrast microscope. Drawings were made with the aid of a camera lucida. One radula of a *Prochaetoderma* species was examined with a scanning electron microscope.

### COMPARATIVE MORPHOLOGY OF ALIMENTARY TRACTS

#### Mouth

The external tissue surrounding the mouth in Aplacophora is usually supplied with mucous cells and nerve strands and the mouth is closed by a sphincter muscle. In some Neomeniomorpha there is a peri-oral fold; in *Gymnomenia* this fold bears numerous cuticular processes, which are extensions of the peri-oral cuticle and presumably receive tactile stimuli (Fig. 2M, N). The cuticle of the peri-oral fold is a continuation of the foregut cuticle, and both are supplied by large mucous glands or masses of mucous cells (ducts were not clearly seen).

The Chaetodermomorpha all have a cuticularized oral shield, divided or undivided and more or less surrounding the mouth opening (Fig. 2D, E, J, L). The cuticle of the oral shield is not part of the epidermal, integumental cuticle (Hoffman, 1949) (Fig. 2A), but is a thickened continuation of the cuticle of the oral tube and buccal cavity in *Scutopus*, *Limifossor*, and *Prochaetoderma* (Fig. 2B, G, K). Nierstrasz (1903) noted the same condition in *Metachaetoderma challengerii*, and Schwabl (1961) considered the oral tube epithelium to be a continuation of the oral shield epithelium in *Falcidens hartmani*. In *Chaetoderma nitidulum* and *Falcidens caudatus* the cuticle of the shield joins that of the oral tube; the latter continues for only a short distance before grading into very dense, long cilia (Fig. 2H, I), which in turn shorten and continue into the buccal cavity (see also Schwabl, 1961).

The epithelial cells underlying the oral shield vary in detail among genera, but certain generalizations seem to hold. There is an abrupt change in epithelial cell type between the cells of the oral shield and those of the oral tube (Fig. 2C, F, arrow); however, the

*nitidulum* the mucous cells form lobes which open at the lateral edges of the oral shield (Hoffman, 1949, and confirmed here).

The oral shield seems to serve both in locomotion and as a sensory organ; it is highly innervated by several precerebral ganglia (Hoffman, 1949; Salvini-Plawen, 1972a) (Fig. 2B).

One specimen of *Scutopus megaradulatus* shows that although the thickest part of the oral shield bends away ventrally from the mouth, it is continuous with and surrounds the mouth opening (Fig. 2D), an observation that does not agree with the original description (Salvini-Plawen, 1972b).

#### Buccal Cavity

*Gymnomenia* n. sp. As in many Neomeniomorpha, the foregut appears to be suctorial and a buccal cavity as such is not distinct from the rest of the foregut (Fig. 1A). Two sphincters and numerous circular muscles surround the foregut, in addition to the anterior sphincter that closes the mouth. The radula lies between the two posterior sphincters; the posteriormost one defines the juncture of fore- and midgut. Masses of goblet cells surround the foregut, but there is no ventral pair of salivary glands (Fig. 4F). Between the mouth and the first sphincter the secretory cells are basophilic; between the first and second sphincters they stain orange (Orange II counter-stain).

*Scutopus* (*S. megaradulatus*). The dorsal half to two-thirds of the buccal cavity is lined by tall goblet cells bearing a thick striated cuticle (Fig. 3A). The goblet cells secrete large yellow granules and empty through the cuticle; they occur in all stages of vacuolization (Fig. 3I). A pair of simple tubular salivary glands 150  $\mu$ m in length lies ventral to the buccal cavity; they empty near their posterior ends laterally into the buccal cavity at the level of the anterior end of the radula. The tip of the buccal mass does not lie free in the buccal cavity; thus there is no sublingual cavity, and the odontophore remains within the main space of the haemocoel (Figs. 1B, 3A).

*Limifossor* (*L. talpoideus*). The large odontophore tip lies free in the cuticle-lined buccal cavity, and there is a spacious sublingual cavity (Figs. 1C, 3B). Tall goblet cells with large yellow granules similar to those in *Scutopus* line the buccal cavity laterally and dorsally; ventrally the goblet cells are scat-

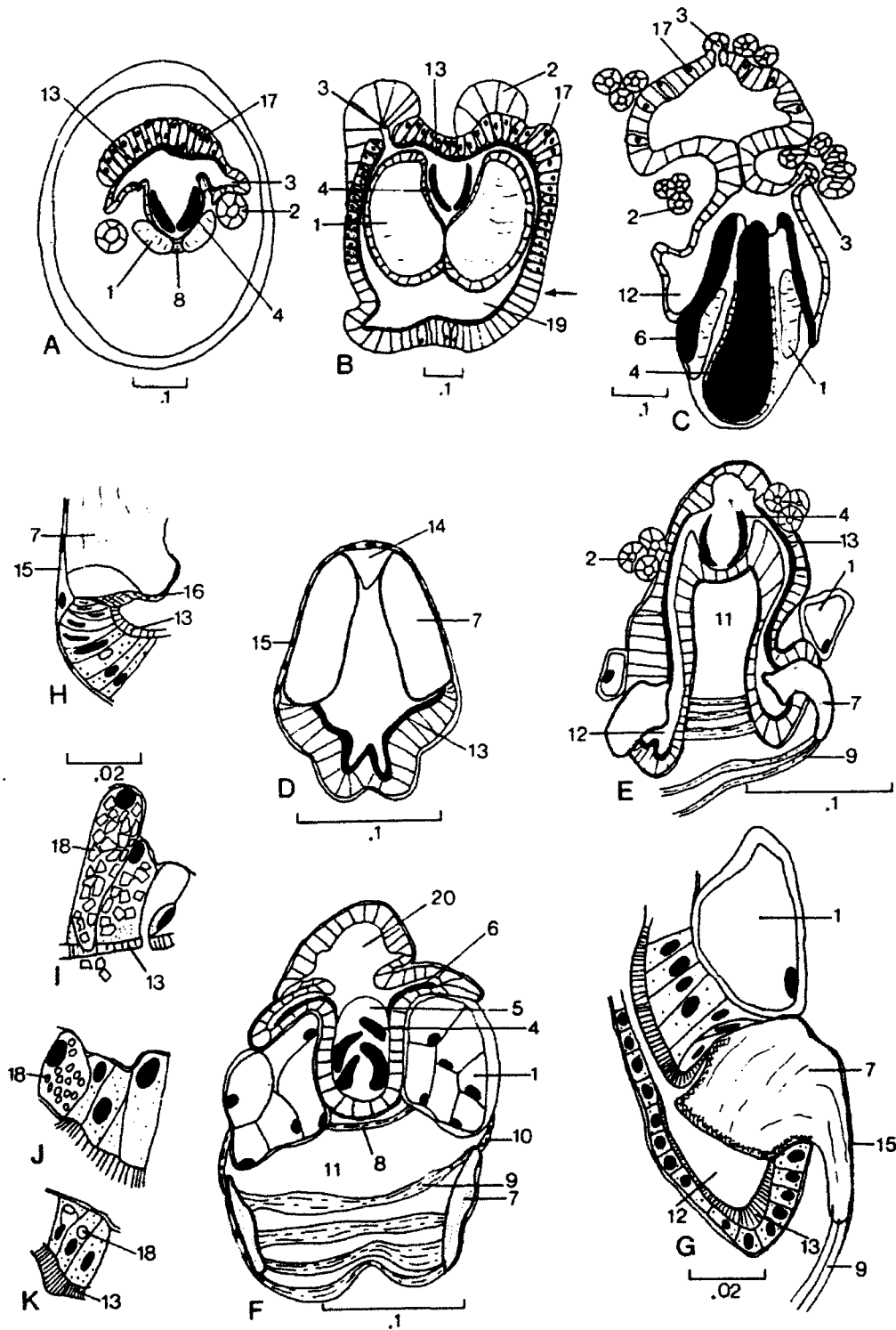
tered. A pair of tubular salivary glands empties dorsally into the buccal cavity near the radula tip; they originate anteriorly and rather far ventrally (arrow, Fig. 3B).

*Prochaetoderma* (spp. y, p). The spacious buccal cavity is lined by a thick cuticle (Fig. 3D, E). The epithelium is formed of medium-high columnar to cuboidal cells filled with fine granules; some have a single large yellow secretory body with or without connection to a vacuole (Fig. 3K). The anterior part of the buccal cavity is dominated by a pair of cuticular jaws which hold the mouth open during feeding (Kowalevsky, 1901; unpublished data) (Figs. 1D, 3D). The jaws are abutted by the epithelium of the buccal cavity; laterally they lie directly against basement membrane (Fig. 3H). Thus, they are not part of the buccal cavity cuticle as reported by Schwabl (1961) and are not homologous to gastropod jaws but are unique structures among the molluscs. The bases of the jaws lie wholly within the haemocoel (Fig. 3F; cf. Fig. 7B, C). At the point where their bases join the long anterior ends, the jaws pierce through the buccal cavity wall (Figs. 1D, 3E, G). The cuticle of the jaws is perhaps secreted at the point where the jaws are abutted by the epithelium of the buccal cavity, as indicated by a change in epithelial cell type and by the direction of the striations in the jaws (Fig. 3G, H). Although the major part of the jaws lies within the buccal cavity, they appear to have originated as part of the odontophore mass in the haemocoel (see below under *Radula*).

The tip of the odontophore lies free in the buccal cavity, and the lateral buccal pouches are deep (Fig. 3E). A pair of salivary glands with compound tubules opens dorsally near the beginning of the short esophagus.

*Chaetoderma* (*C. nitidulum*). The epithelium of the spacious buccal cavity is formed by tall, brush-bordered columnar cells containing fine granules; there are also scattered goblet cells with large yellow secretions (Fig. 3C, J). Two pairs of salivary glands with compound tubules open laterally and dorsally into the buccal cavity, one pair at the level of the tip of the radula, the other just anterior to the esophagus (as reported by Wirén, 1892). The odontophore lies free in the buccal cavity for one-half or more of its length.

*Falcidens* (*F. caudatus*). The buccal cavity is similar to that of *Chaetoderma*, but is less capacious. There are perhaps also two pairs of salivary glands; however, ducts were not clearly seen for the dorsalmost pair.



## Radula

The aplacophoran radula has been shown throughout the literature to be very diverse in form, and far more plastic than the gastropod radula. However, there are certain structures common both to aplacophorans and other mollusks.

All isolated radulae that I have studied, except those of the Chaetodermatidae, have a discrete radular membrane with attached distichous rows of teeth issuing from a radular sac, which is a diverticulum of the buccal cavity known to secrete the radular membrane and teeth in gastropods (Fretter & Graham, 1962) and appearing to do so in Aplacophora. There is no evidence for a primitive so-called "basal membrane" that is part of the foregut cuticle and different in some way from a true radular membrane (Boettger, 1956; Salvini-Plawen, 1972a). The radular membrane is supported by an odontophore which lies in the haemocoel. There are one or more pairs of bolsters formed of connective tissue and muscle, or of chondroid tissue, or perhaps of collagen and muscle; in one case there is cuticularization. Protractor and retractor muscles run between the odontophore mass and the body wall, and presumably all aplacophoran radulae can be protracted to, or through, the mouth. In gastropods, muscles that run between a subradular membrane and the bolsters move the radula itself (Graham, 1973); in Aplacophora a subradular membrane is usually, but not always, lacking. The radula musculature has been described for only a few aplacophoran species and will not be described here except for a few particular cases. A bending plane may be either present or lacking; if present, there is no fixed position along the odontophore from genus to genus where it is situated.

*Gymnomenia* n. sp. The tiny radula of *Gymnomenia* was overlooked in the original description of the genus (Odhner, 1921) (Fig. 4); it is considered to be secondarily reduced by Salvini-Plawen (1978). There are about 28

rows of hooked distichous teeth, each with two median denticles in various stages of being tanned. None of the teeth show wear. Each tooth is attached to the radular membrane for one-half its length (Fig. 4B, C). In interference contrast, the radular membrane was seen to be continuous (a) between the teeth of each row as a slight ridge (Fig. 4B, C), which in turn runs down the length of the radula; (b) along and slightly below the base of the teeth lengthwise along the radula (Fig. 4A); and (c) lengthwise along the radula at the level of the denticle in the middle of each tooth (Fig. 4D). Thus, the radular membrane is a continuous sheet which appears to be fused medially; it bears two longitudinal rows of well-affixed teeth. Teeth attached so firmly to the radular membrane can have only limited movements.

The orientation of the radula is similar to that described for *Genitoconia* (Salvini-Plawen, 1967a). The fore-end of the radula is positioned dorsoventrally, where it lies in a blind sheath (Fig. 4E, F). About two-thirds of the distance towards the newest formed teeth in the radular sac there is a bending plane, over which the teeth open into the foregut. The short dorsal radular sac is perhaps bifid as in other Wreniidae, as indicated by the medial ridge of the radular membrane, but further histologic material is needed for substantiation.

The base of the fore-end of the radula lies against the connective tissue (? and commissure), defining the pedal sinus (Fig. 4F); directly beneath this, in the sinus, are about seven calcareous statoliths, each produced by a statocyst (Fig. 4G). In *Genitoconia*, Salvini-Plawen (1967a) described a pedal commissure sac with vesicles which he considered perhaps to be a balancing organ ("ein statisches Organ").

The odontophore protractors and retractors have been described for *Genitoconia* (Salvini-Plawen, 1967a), but the exact manner in which they operate the radula is not clear. The function of the enclosed fore-end of the radula

FIG. 3. Buccal cavity in Chaetodermomorpha. A, I: *Scutopus megaradulatus*; B: *Limfossor talpoides*, arrow indicates level of blind end of salivary gland; C, J: *Chaetoderma nitidulum*; D-H, K: *Prochaetoderma* sp. y. Scales in mm. 1, bolster; 2, salivary gland; 3, opening of salivary gland into buccal cavity; 4, radular tooth (diagrammatic); 5, radular membrane; 6, subradular membrane; 7, jaw; 8, ventral approximator of bolsters; 9, ventral approximator of jaw; 10, tensor between bolster and base of jaw; 11, lumen of odontophore; 12, buccal pouch; 13, cuticle of buccal cavity; 14, dorsal cuticular membrane between distal end of jaws; 15, basement membrane; 16, deeply staining portion of jaw cuticle; 17, goblet cell; 18, large yellow granule; 19, sublingual cavity; 20, esophagus.

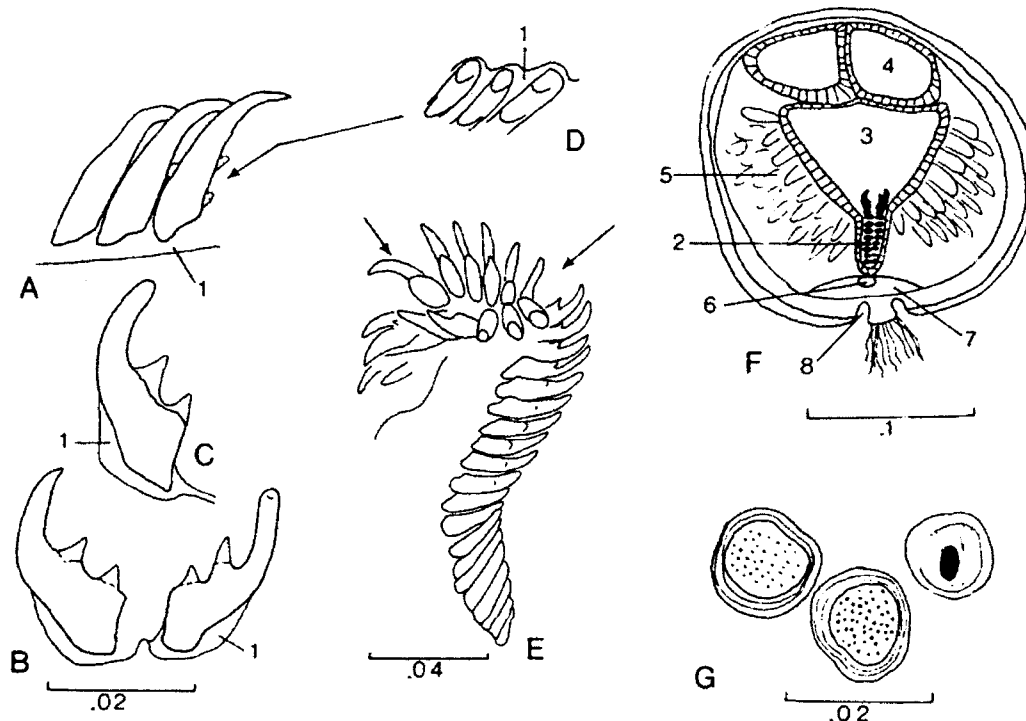


FIG. 4. Radula and statoliths of *Gymnomenia* n. sp. A-D: radular teeth; A, lateral view; B, C, anterior view; D, median view at level of middle denticle indicated by arrow on A; E: radula, lateral view, dorsal at top, anterior to right, most recently formed teeth to left, teeth between arrows exposed in pharynx; F: cross-section showing exposed teeth in foregut and sheath around fore-end of radula resting against statocyst. G: two statoliths and a statocyst cell filled with amorphous substance. Scales in mm, A-D at same scale. 1, radular membrane; 2, radula; 3, foregut; 4, paired dorsal caecum of midgut; 5 goblet cells; 6, statocyst; 7, pedal sinus; 8, pedal pit.

is not known; it may act as a supporting rod-like structure. The proximity of the radula to the statocysts of the pedal sinus may or may not indicate a direct relationship between them. The exposed teeth perhaps are able weakly to tear at soft tissue as it is sucked into the foregut, and very probably serve to move food backwards toward the midgut.

*Scutopus* (*S. robustus*, *S. megaradulatus*). The radula is formed of seven or more pairs of teeth in a straight, nearly anteroposterior position, with the distal ends of the teeth lying anteriorly to the proximal ends (Figs. 5A, B, 11D). Thus, the older of any two rows of teeth lies beneath and anterior to the younger, and the odontoblasts lie on the dorsal side of the radular sac. There is no bending plane. The teeth of *S. megaradulatus* and *S. robustus* are thick and massive, with pointed tips and many large median denticles which curve ventrally and posteriorly (Fig. 5D). From histo-

logic sections and whole preparations the radular membrane was seen to be formed of two longitudinal bands connected only between each pair of teeth (Fig. 5C). Each band extends laterally along the side of each tooth, but these extensions are not connected (Fig. 5C, D). Thus, the teeth are free to slide past each other, perhaps moved by the ventral tensor (Fig. 5A); they can also be closed by a large dorsal approximator muscle running between the anterior pair of bolsters (Fig. 5A, B). These rather limited possibilities for movement combined with the absence of a bending plane and of a sublingual cavity suggest a simple shovelling or pulling in of food. The radula probably cannot be protruded very far beyond the end of the radular sac, and the teeth do not show any wear.

*Limifossor* (*Limifossor* n. sp., *L. talpoid-eus*). The radula with its massive odontophore was well described by Heath (1905),



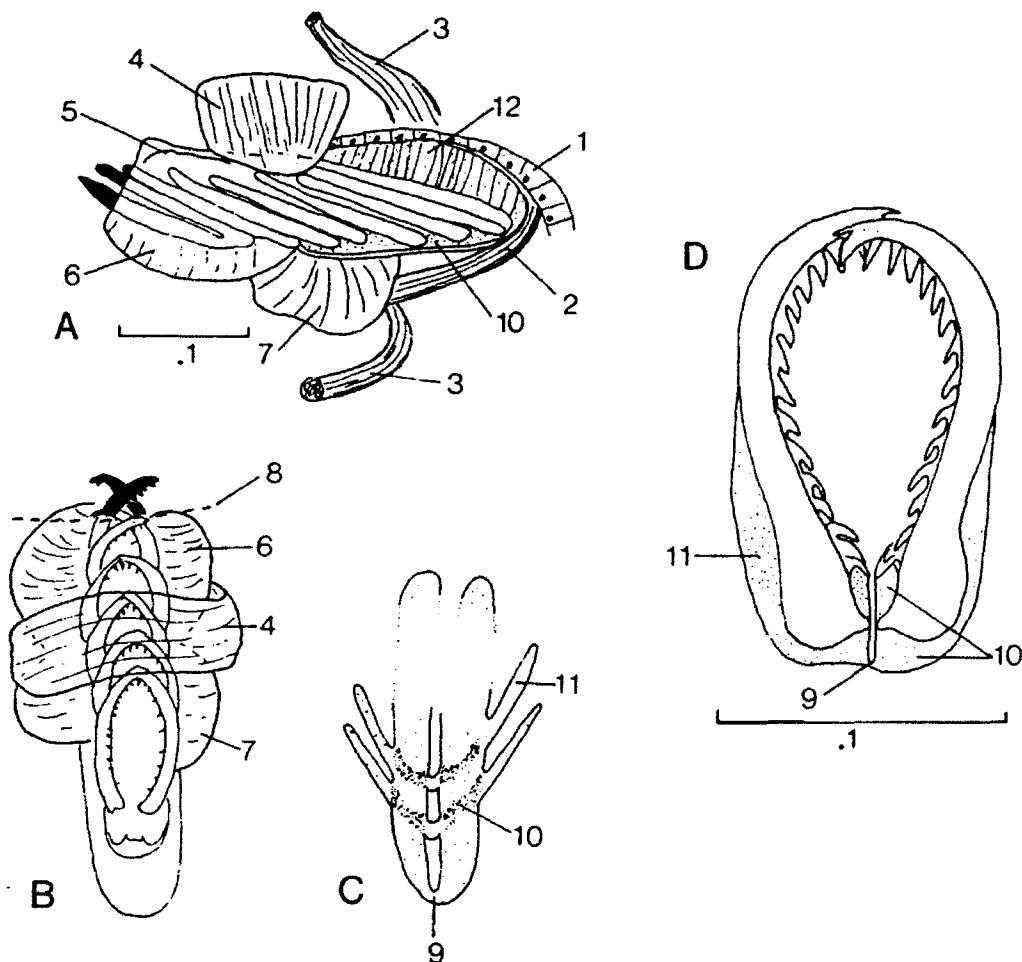


FIG. 5. Radula of *Scutopus*. A, B, D: *S. robustus*; C: *S. megaradulatus*. A, lateral view of buccal mass, anterior to left, teeth beyond radular sheath black; B, dorsal view, anterior end at top; C, diagrammatic representation of radular membrane; D, pair of radular teeth. Scales in mm, A and B at same scale. 1, midgut epithelium; 2, ventral tensor muscle; 3, protractors; 4, dorsal approximator of bolsters; 5, radular sac; 6, anterior bolster; 7, posterior bolster; 8, anterior limit of radular sac; 9, radular membrane connecting pair of teeth; 10, radular membrane attached to base of teeth; 11, lateral extension of radular membrane; 12, odontoblasts of radula.

who illustrated the musculature and watched the radular movements of living animals. A few observations may be added to his.

As Heath noted, the radular membrane is a continuous sheet only at the posterior end of the radula; farther anteriorly it splits along the midline (arrow, Fig. 6B) and continues as two bands. The radular membrane extends for a short distance up the lateral side of each tooth, and these lateral extensions are in connection along the radula (Fig. 6A, C). The teeth are massive, with long lateral hooks and shorter median hooks turned posteriorly (Fig.

6C, D); the bases have a thickened ridge posteriorly. The teeth are set close to each other along the radula; each tooth thus appears to act as a fulcrum for the next posterior one (Fig. 6C, D). There is a large mass of muscle fibers, the tooth adductor, that Heath (1905) found to be responsible for moving the opposed teeth toward each other (Fig. 6B); there is a dorsal approximator of the bolsters, present as in *Scutopus*, which is also probably important in bringing the two rows of teeth together (Fig. 6B). None of the teeth show wear.

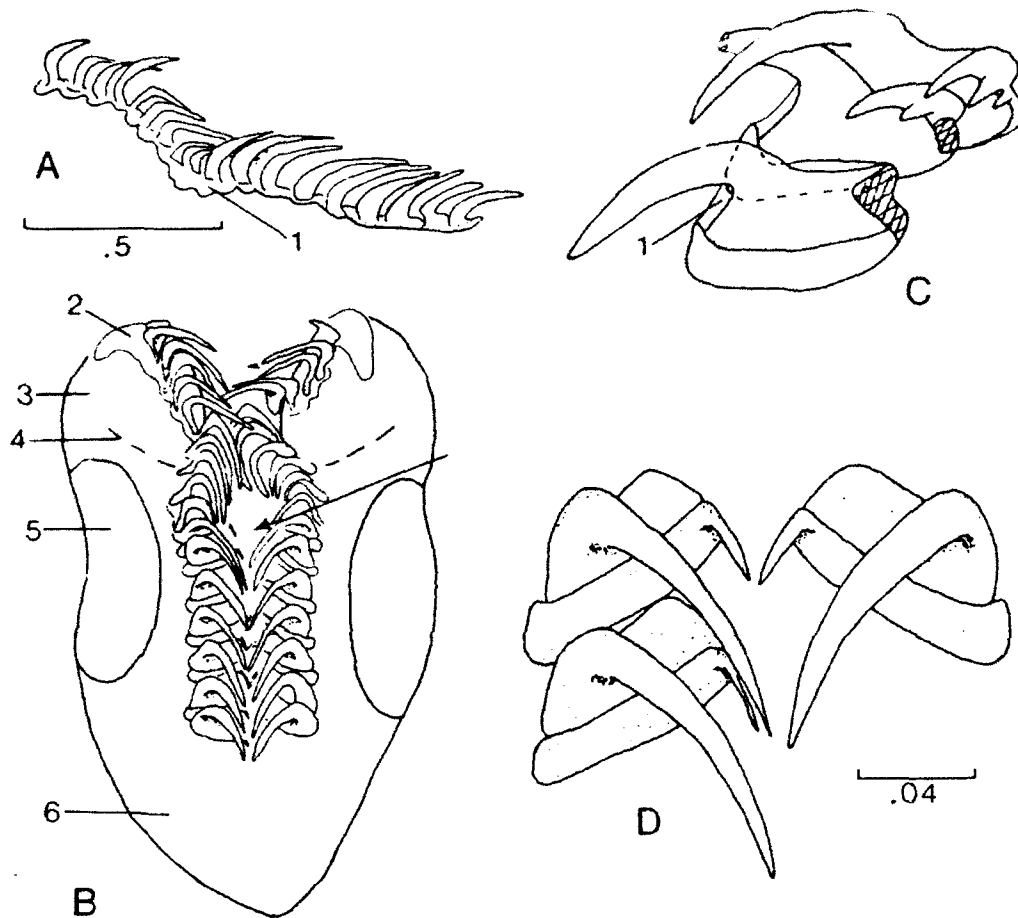


FIG. 6. Radula of *Limifossor* n. sp. A: lateral view of radula, dorsal at top, anterior to left; B: dorsal view of radula and odontophore, anterior at top; arrow indicates point where radular membrane splits into two bands; C, D: oblique and dorsal views of teeth in natural position. Scales in mm, A-B and C-D at same scales. 1, radular membrane; 2, subradular membrane?; 3, odontophore mass; 4, anterior limit of radular sac; 5, attachment of dorsal approximator of bolsters; 6, area of large tooth adductor muscle.

A certain amount of rotation of the teeth is possible, as shown in Figure 6B. These movements are made possible by (a) the median split in the radular membrane, which frees the two longitudinal rows anteriorly, (b) the use of each tooth as a fulcrum by the next posterior one, (c) the presence of a rudimentary bending plane, (d) the possible existence of a subradular membrane for tensor insertion, and (e) a deep sublingual cavity, which frees the entire buccal mass from the haemocoel (Fig. 3B). Heath reported that the odontophore swept past the teeth when the mouth was open. Certainly the radular teeth are able to go through a more complicated set

of movements than can those of *Scutopus* or *Gymnomenia*. Less certain is whether the radula is used for tearing or simply is an improved form of rake.

*Prochaetoderma* (spp. y, p, c). Kowalevsky (1901) figured the isolated distichous radula of *Prochaetoderma raduliferum*; some details can be added.

Most noticeable are the two large cuticular jaws that nearly fill the space in the head (Fig. 7A-C). Anteriorly they are connected by a membrane (Figs. 3D, 7C); posteriorly within the haemocoel a large bundle of muscle fibers runs between their bases, and a small fiber runs between each base and the chon-

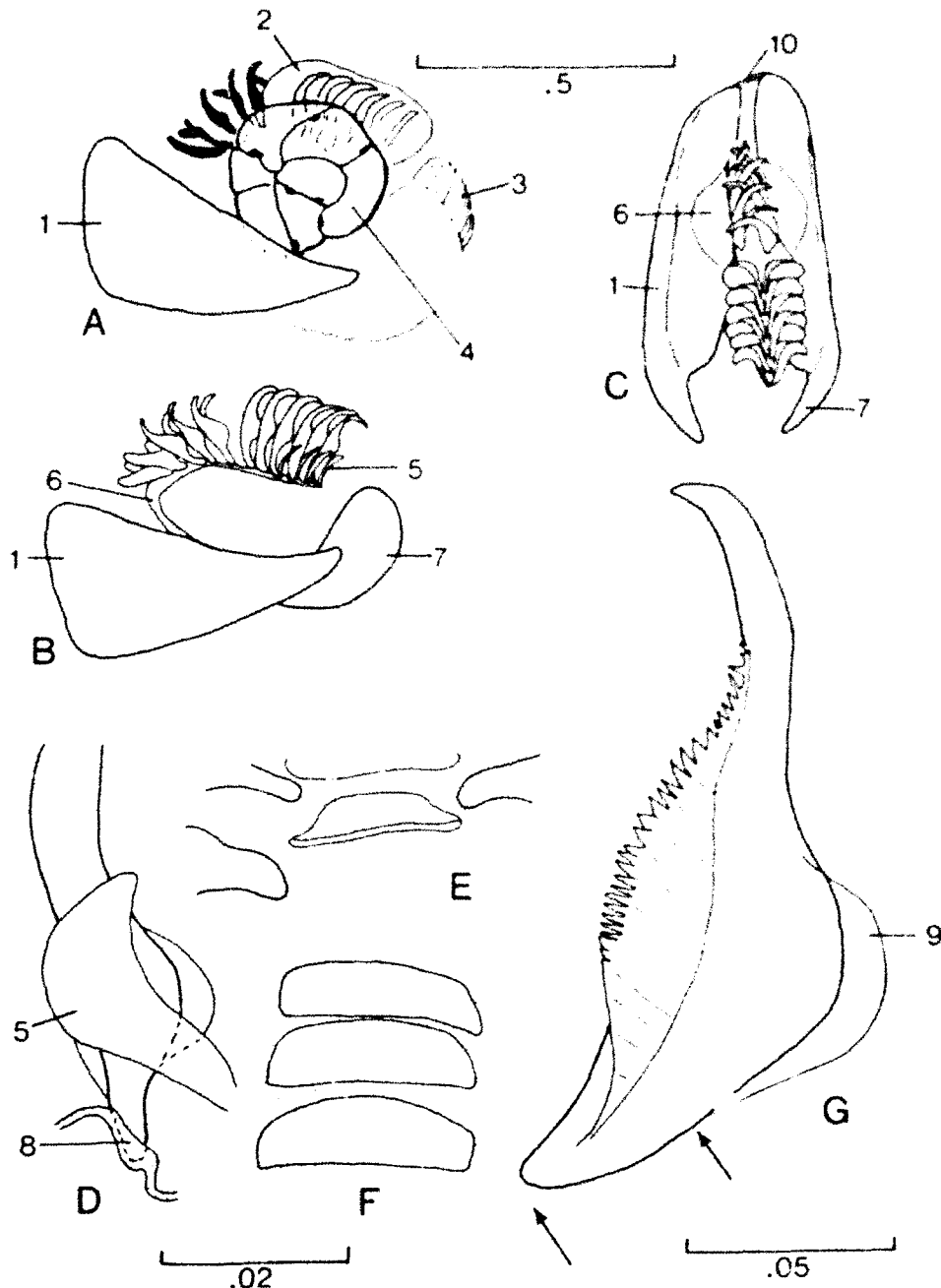


FIG. 7. Radula of *Prochaetoderma*. A-F: *Prochaetoderma* sp. y; G: *Prochaetoderma* sp. p. A, lateral view of jaws, radula, and odontophore, anterior to left; B, same as A, tissue removed; C, dorsal view of B, anterior at top; D, base of tooth, with lateral tooth-like extension and radular membrane in darker stippling; E: oblique view of central plate, or tooth, in relation to proximal ends of teeth; F: row of central plates, anterior at top; G: single radular tooth with membranous denticulate medial brush and lateral membranous wing, attachment to radular membrane between arrows. Scales in mm, A-C and D-F at same scales. 1, cuticular jaw; 2, radular sac; 3, tensor muscles between jaws; 4, chondroid bolster; 5, toothlike lateral extension of radular membrane; 6, subradular membrane; 7, case of jaw which lies within haemocoel; 8, radular membrane; 9, membranous wing of radular tooth; 10, dorsal cuticular membrane.

droid bolster immediately dorsal to it (Fig. 3F). The jaws serve to hold the mouth open, and the radula is protruded between them. The musculature which protracts and retracts the jaws has not been described.

The radular membrane is a continuous sheet to which only the tips of the proximal ends of the teeth are attached (Fig. 7D, G; observation substantiated by scanning electron microscopy). Laterally the membrane is drawn out into a tooth-like extension beside each tooth; the extension is not attached to the tooth but appears to support it in some manner (Figs. 7B, D, 11A). A bending plane lies at the anterior end of the odontophore (Fig. 7B). Uniquely in the Aplacophora, a central plate, or tooth, lies between the bases of each pair of teeth (Fig. 7E, F). The four to six pairs of anterior teeth are crossed and used in feeding (Figs. 7C, 11C); the anterior-most pair are worn (Fig. 11B). The posterior teeth, which probably remain within the radular sac, seem to function as a backstop for food particles carried between the membranous median brush-like extensions of the teeth (Figs. 7G; 11C). There is a subradular membrane, distinct from the radular membrane (Figs. 3F, 7B).

The radula of *Prochaetoderma* appears to reduce the size of food material by rasping before ingestion on the following evidence: (a) the mouth can be held open by the jaws probably independent of radular protrusion; (b) the teeth can articulate, for they are free of the radular membrane laterally and there are median supportive teeth; (c) the chondroid tissue of the bolsters provides a stiff structure to work beneath the protruded radula; (d) there is a bending plane at the anterior end of the odontophore over which the teeth can be articulated; (e) the anterior teeth are worn. Kowalevsky (1901) described the protracted, anterior crossed teeth in living animals as projecting through a wide-open mouth and constantly in motion as if to seize something.

*Falcidens* and *Chaetoderma* (several species). The very specialized radulae of the Chaetodermatidae (Fig. 8) have already been described in detail from isolated preparations (Scheltema, 1972). Paired denticles or lateral projections attached to the end of a cone-shaped rod presumably act as grasping pincers; tensors run between them and the bolsters (Schwabl, 1961; Ivanov, 1979) (Fig. 8C). There are three published interpretations of the cone-shaped structure: it represents a fused radula (Scheltema, 1972); it is a greatly

thickened basal membrane (Salvini-Plawen, 1972a); it is one of three teeth of a monosegmental radula (Ivanov, 1979). The cone lies within an epithelial sheath, perhaps the radular sac (Fig. 8C), and is secreted at its thick, ventral end. The identity of growth lines in the cone of *Chaetoderma* with those in *Prochaetoderma* jaws is highly improbable (Salvini-Plawen & Nopp, 1974), for the jaws appear to be a part of the odontophore mass

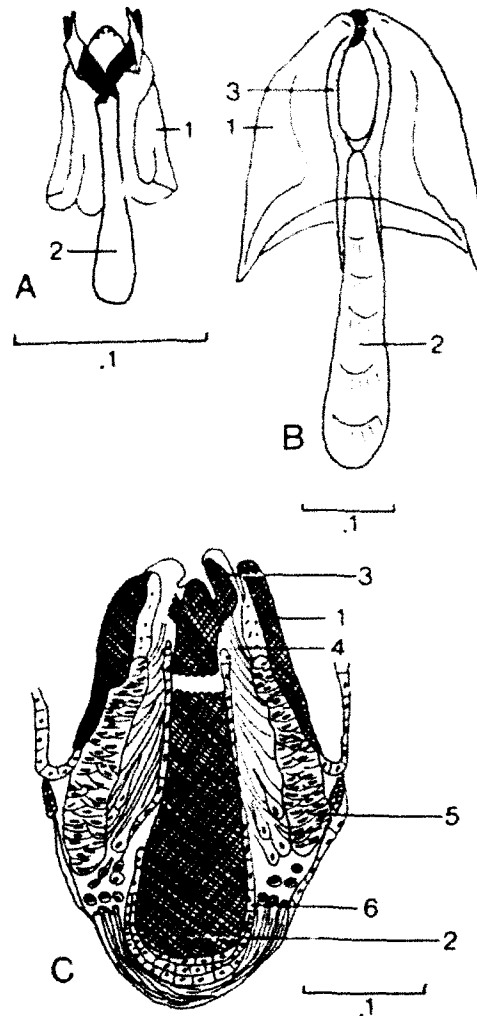


FIG. 8. Radulae of *Chaetoderma* and *Falcidens*. A: *Falcidens* n. sp.; B: *C. abidjanense* (from Scheltema, 1976); C: *C. nitidulum*, histologic section. Scales in mm. 1, cuticle surrounding buccal mass (subradular membrane?); 2, cone-shaped tooth; 3, lateral projection; 4, tensors of lateral projection; 5, bolster; 6, epithelium surrounding cone-shaped tooth (radular sac?).

within the haemocoel and are not underlain by epithelium (cf. Figs. 3D, E, F, 8C).

### Esophagus

The esophagus is defined as that part of the foregut forming a tube above the radula and connecting the buccal cavity and stomach. Its epithelium is differentiated from the epithelium of both the buccal cavity and the stomach.

*Gymnomenia* n. sp. An esophagus is lacking in *Gymnomenia* but not in all Neomeniomorpha, although Odhner (1921) considered the posterior pharynx of *G. pellucida* to be an esophagus.

*Scutopus* (*S. megaradulatus*). The buccal cavity opens dorsally into a short, wide esophagus formed of low cuboidal epithelium with a brush border; the cells are filled with fine, yellow granules. A short distance posteriorly the lateral walls acquire folds, and the ventral wall thickens. The folds merge dorsally and become ciliated; posteriorly they coalesce into a typhlosole that continues into the stomach.

*Limifossor* (*L. talpoideus*, *L. ?fratula*). As described by Heath (1905), the esophagus is a long, ciliated, narrow tube with several longitudinal folds; the cells are filled with granules. Dorsally the ciliated epithelium is continued into the stomach.

*Prochaetoderma* (sp. y, p). The esophagus is extremely short and bears no cilia; however, Schwabl (1963) reported a ciliated esophagus in *P. californicum*.

*Falcidens* (*F. caudatus*). The esophagus is discernible from the buccal cavity only by its long, slender goblet cells which lie between the buccal cavity and stomach.

*Chaetoderma* (*C. nitidulum*). Cells with a brush border line a muscular esophagus. At the entrance to the stomach there are very long, slender goblet cells but no cilia; these coalesce dorsally and become the ciliated typhlosole in the stomach.

### Midgut

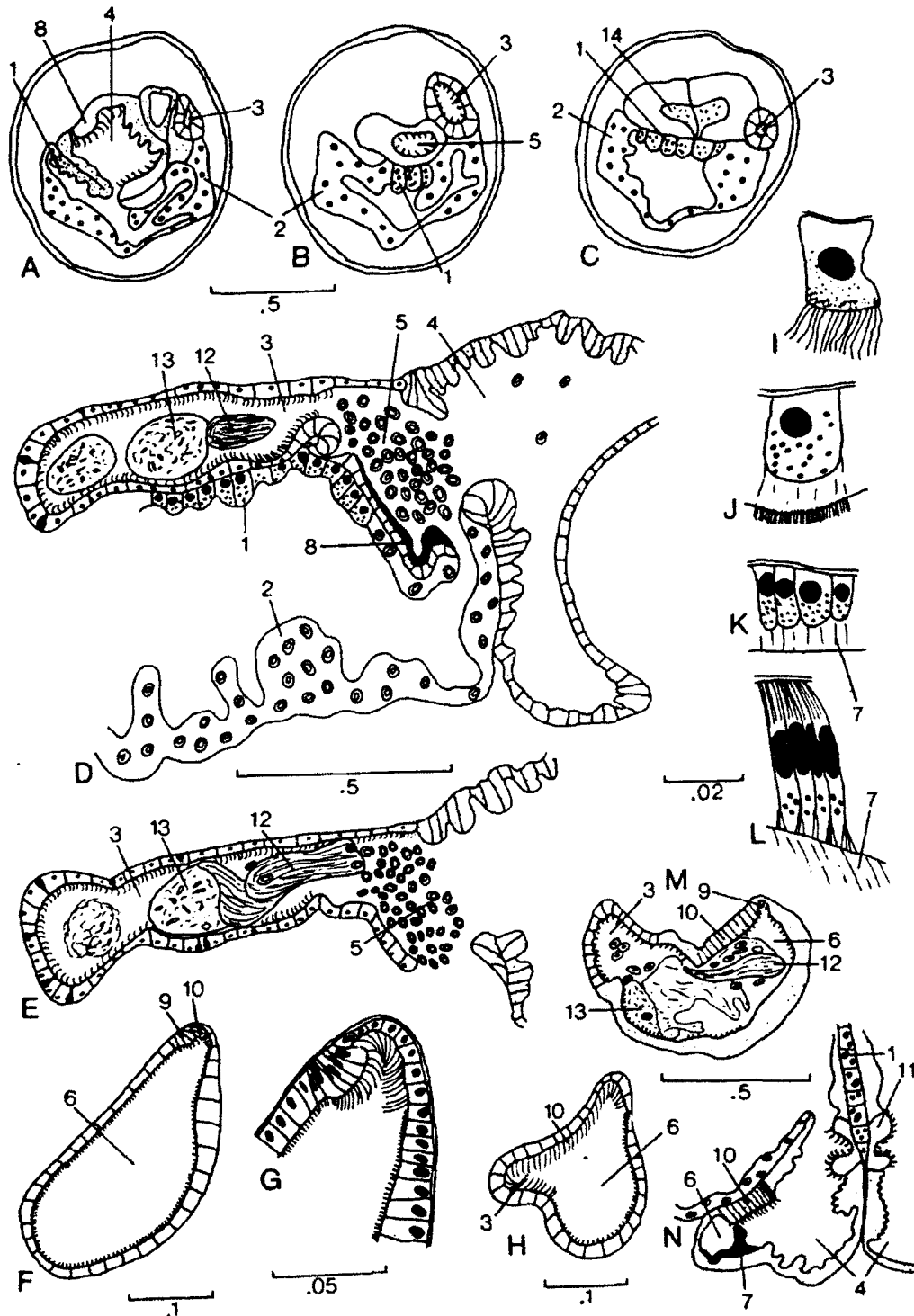
Neomeniomorpha. The stomach is a single wide tube interrupted laterally at regular intervals by the dorsoventral musculature (Fig. 1A). In most Neomeniomorpha there is an anterior-dorsal paired or unpaired caecum (Fig. 4F). The cell types of the midgut are not described here. A dorsal ciliated tract or fold runs the length of the midgut and leads into a short posteriorly placed, ciliated intestine

(Pruvot, 1891; Salvini-Plawen, 1978); it was not seen in *Gymnomenia*, however.

Chaetodermomorpha. All members of the Chaetodermomorpha investigated here have a stomach, a sac-like ventral digestive diverticulum that opens into the posterior end of the stomach, and a long ciliated intestine that follows a bend in the posterior stomach. Nierstrasz (1903) reported that *Metachaetoderma challengerii* lacked a separate midgut gland in the one incomplete specimen he examined, but this observation needs to be repeated. Except in *Prochaetoderma* there is either a dorsal ciliated typhlosole or a groove that runs down the stomach to the ciliated intestine. The epithelial cells lining the stomach are homogeneous and contain granules; cell shape varies among genera and species. The cells of the digestive gland are unique among mollusks: the dorsal wall is lined by a band of cells packed with coarse yellow granules (lacking in *Prochaetoderma*) (Fig. 10H); laterally and ventrally are cells which secrete large basophilic spheres (Fig. 10G). A mucoid or proteinaceous rod is present in all genera except *Prochaetoderma*, but its position in the gut varies.

*Scutopus* (*S. megaradulatus*, *S. robustus*). The stomach is long and divided by septa which do not run its entire length. These do not appear to be the same as the outpouchings that Salvini-Plawen (1972a, fig. 16) illustrated for *S. ventrolineatus* related to dorsoventral musculature. The granular cells of the stomach epithelium have a striated or brush border; anteriorly they are low and cuboidal, but farther posteriorly they become high and club-shaped (Fig. 10A, B). A strip of the stomach epithelium passes into the digestive diverticulum and continues there as a dorsal band of granular cells with greatly coarsened granules (Figs. 9A-C, 10B, H, 11D). A dorsal ciliated typhlosole (Fig. 10A, C) runs from the esophagus to the intestine; there is a second ciliated typhlosole arising at the base of the stomach that also runs to the intestine. A patch of ciliated cuboidal cells with densely staining borders opposes the bend that joins stomach and intestine (Fig. 9A, I).

In three specimens out of a sample of 19 *S. robustus*, the stomach epithelium was nearly colorless owing to the lack of cell granules. Dissection of two of these colorless specimens revealed that the stomach contained several solid, proteinaceous (stained by rose Bengal), acellular, parallel rods which were presumably formed by secretions from the



septate stomach (Fig. 11E). Crystals of about 40  $\mu\text{m}$  adhered to the outsides of the rods; these crystals became more densely packed posteriorly. Both rods and crystals passed into the anterior intestine; farther posteriorly the crystals, but not the rods, formed part of a fecal mass. The crystals may be organic, as they dissolved in dilute HCl (but not  $\text{NH}_4\text{OH}$ ) and broke down into an amorphous yellow mass when subjected to pressure by squeezing them beneath a glass coverslip. In *S. megaradulatus* sections, the stomach was empty and the stomach cells were packed with granules; there was only a short mucoid rod at the anterior end of the intestine.

Fecal material in *Scutopus* is formed into a long spindle-shaped mass along a straight intestine (Fig. 1B).

*Limifossor* (*L. talpoideus*, *L. ?fratula*). The epithelium of the very short (*L. talpoideus*, Fig. 1C) or very long (*L. ?fratula*) stomach are formed of tall (former) or short (latter) cuboidal granular cells with a striated or brush border. A dorsal typhlosole runs from the esophagus to the intestine. At the posterior bend between the stomach and intestine in *L. talpoideus* the cells are thickly ciliated (?brush border) and have a thick amorphous border resembling cuticle (Fig. 9D, J). Within the anterior ciliated intestine (interpreted originally as a style sac, Scheltema, 1978) is a mucoid rod (Fig. 9D, E). The digestive diverticulum is long. Fecal material is formed into oblong masses along a straight intestine.

*Prochaetoderma* (spp. *y*, *p*). The stomach is lined by low cuboidal cells probably with a cuticular border; cilia are lacking. The short digestive diverticulum lacks a dorsal band of granular cells and is formed only of secretory cells which are modified from the type found in other chaetoxiids; the cell granules are eosinophilic and there are few basophilic, spherical secretions. There is no mucoid rod. The short anterior section of the intestine may

be bent or straight. Fecal material is formed into discrete spherical masses strung out along a long, convoluted intestine (Fig. 1D).

*Chaetoderma* (*C. nitidulum*). The stomach and digestive diverticulum are long (Fig. 1F). A dorsal typhlosole starts just posterior to the esophagus and runs the length of the stomach and into a style sac (Fig. 9N); only the medial cells of the typhlosole are ciliated anteriorly (Fig. 10E). The stomach epithelium is formed of low cuboidal cells with a striated or brush border; the granular cells of the dorsal band in the digestive diverticulum are very tall with a striated border and were not seen to be in connection with the stomach epithelium. At the base of the stomach there is a thick, hooklike cuticular gastric shield underlain by tall columnar cells which are granule-filled distally and striated basally; fibrils run between the cuticle and cell walls (Fig. 9L, N). The ciliated style sac runs between the stomach and the intestine transversely to the long axis of the body; it contains a mucoid rod in some specimens (Fig. 9M) (see also Scheltema, 1978, fig. 1B). The rod appears to rotate against the gastric shield, inasmuch as food material between the rod and the shield occurs in spiral swirls. The style sac is formed of granular cells with dense, short cilia; a broad ridge borders a groove with longer cilia which continues into the intestine (Fig. 9F-H, M). Fecal material is formed into oblong masses; the intestine is straight.

*Falcidens* (*F. caudatus*). The stomach is short and bilobed (Fig. 1E); its epithelium is formed of low cuboidal cells with yellow granules and a cuticular border (Fig. 10D). A strip of these cells continues, without a cuticular border, into the digestive diverticulum where it becomes the dorsal band of granular cells of that organ. The digestive diverticulum extends broadly to where the body narrows into a "tail."

A dorsal ciliated groove, rather than typhlo-

FIG. 9. Posterior stomach, anterior intestine, and opening of digestive diverticulum in Chaetodermomorpha. A-C, 1: *Scutopus megaradulatus*; D, E, J: *Limifossor talpoideus*; F-H, L-N: *Chaetoderma nitidulum*; K: *Falcidens caudatus*. A-C, cross-section from anterior to posterior, viewed anteriorly; D, E, nearly adjacent sagittal sections, anterior to right; F-H, M, oblique sections through style sac of two specimens, one showing groove (enlarged in G) running into intestine (H) and one with protostyle (M); I-L, morphocline of cells from ciliated to cuticularized at bend between stomach and intestine (I enlarged from A, 8; J from D, 8; K from N, 7). N, oblique view anterior to M at junction of stomach and style sac, showing gastric shield. Scales in mm, A-C, D-E, I-L, M-N, at same scales. 1, dorsal band of granular cells; 2, secretion cells with basophilic spheres; 3, intestine; 4, stomach; 5, bend between stomach and intestine; 6, style sac; 7, gastric shield; 8, specialized cells at bend between stomach and intestine; 9, style sac ridge; 10, style sac groove; 11, dorsal typhlosole; 12, mucoid rod (protostyle); 13, bolus entering intestine; 14, gonad.

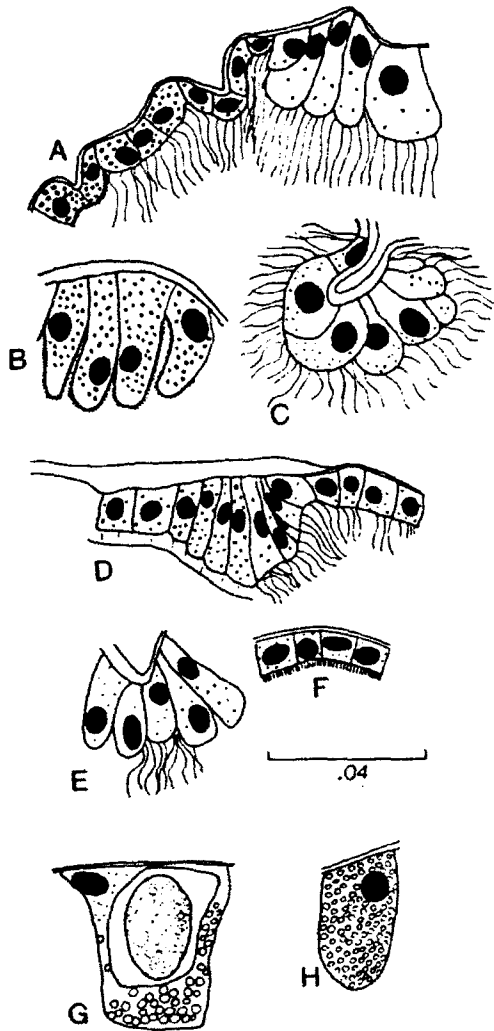


FIG. 10. Cells of alimentary tract in Chaetodermomorpha. A-C, H: *Scutopus megaradulatus*; D: *Falcidens caudatus*; E-G: *Chaetoderma nitidulum*. A-F, granular stomach cells and dorsal ciliated typhlosole or groove (B, C posterior to A); G, digestive gland secretory cell with basophilic sphere; H, cell from dorsal band of granular cells of digestive gland.

sole (Fig. 10D), starts about half way down the length of the stomach and leads to a hook-like gastric shield (Scheltema, 1978, fig. 1C), and thence continues into a style sac. A second, ventral ciliated band starts at about the level of the gastric shield and joins the dorsal typhlosole to form a style sac with a mucoid rod and ciliated ridge bordering a groove. The rod appears to rotate against the gastric shield. Schwabl (1961) described and figured

schematically the gastric shield and style sac for *F. hartmani* without considering them as such, although referring to the style sac as "caecum-like"; a mucoid rod is not mentioned. The cells underlying the gastric shield are cuboidal with large granules distally (Fig. 9K). The style sac is transverse to the body axis (Fig. 1E).

The intestine is convoluted and filled with spherical fecal masses.

#### Diet

The diet of the species under discussion is based on stomach contents. Not available to me at this time of writing is Salvini-Plawen's work (in press) on diet (see Literature Cited).

*Gymnomenia* n. sp. As in most Neomeniomorpha, there are many unexploded nematocysts within the cells of the midgut; *Gymnomenia* is therefore considered to feed on Cnidaria.

*Scutopus*. The diet is not known; fecal material contains organic (?) crystals and perhaps sediment particles. The radula morphology suggests that the diet is particle-size dependent, probably detritus.

*Limifossor*. The diet is not known. Fecal material contains very small bits of unidentified frustules, spicules and other hard parts of organic origin. Although *Limifossor* has usually been considered a carnivore (Heath, 1905; Salvini-Plawen, 1975), it seems quite as likely from radula morphology that it is a detritivore and possibly particle-size dependent.

*Prochaetoderma*. The diet seems to be a wide variety of both prey and organic debris. The stomach of several specimens hold Foraminifera with sand tests (?*Saccorhiza*), crustacean parts, radular teeth of smaller *Prochaetoderma*, and bits of unidentified organic remains; much of the food material still contains stained cytoplasm. There are very few sand grains.

*Chaetoderma* and *Falcidens*. The Chaetodermatidae are considered to be selective carnivores, taking in entire Foraminifera, "worms," small snails and other unidentified organisms which are found in the stomach with stained cytoplasm. Ivanov (1979) has figured the action of feeding. *C. nitidulum* can be a contaminant in laboratory cultures of living Foraminifera upon which they will feed (B. Christensen, personal communication). It is not known whether members of the Chaetodermatidae also feed on organic debris. There are few sand grains in the gut.



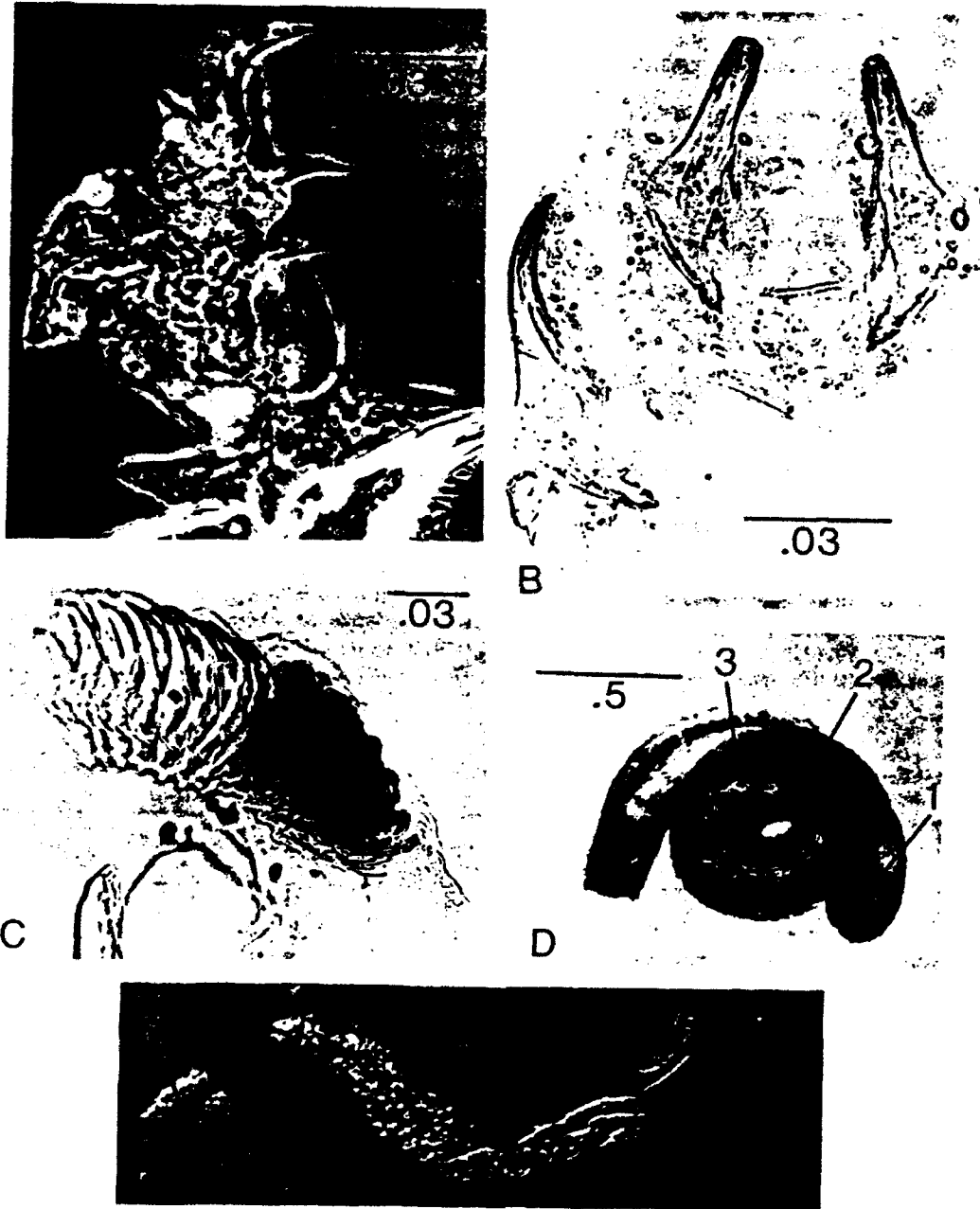


FIG. 11. Radula of *Prochaetoderma* sp. y (A-C) and alimentary tract of *Scutopus robustus* (D, E). A: lateral tooth-like extensions of radular membrane; B: worn anterior pair of denticles; C: food material caught in crossed pairs of anterior teeth, held against posterior 6-7 pairs touching at distal tips; note darkened, tanned distal tips; D: entire preserved specimen in transmitted light; E: proteinaceous rods with adhered crystals dissected from stomach and intestine of a specimen without dark granules evident in D. Scales in mm. 1, radula; 2, darkly pigmented stomach; 3, band of granular cells passing from stomach to dorsal wall of digestive gland; 4, rods from anterior stomach; 5, rods and crystals at base of stomach and entrance into intestine; 6, fecal material.

## DISCUSSION

## Phylogenetic Considerations: Intra-class

The Neomeniomorpha and Chaetodermomorpha are considered by me to be subclasses belonging to the class Aplacophora (Scheltema, 1978) and their great specialization of acquiring a worm shape to have evolved as a single event before evolution of the molluscan shell (i.e., a shared derived character state). The chaetoderm oral shield was thought by Hoffman (1949) to be homologous to the outer wall of the ventral foot furrow of the neomeniomorphs (homology is not with the foot sole, Scheltema, 1978). This homology is not substantiated by the observation that the chaetoderm oral shield is formed from cuticularized gut epithelium that has come to lie externally like lips (Fig. 2). Moreover, the mucous cells of the oral shield in the primitive species *Scutopus megaradulatus* are diffuse and do not occur in lobes as required by this homology (Hoffman, 1949). Therefore the separation of the Chaetodermomorpha (Caudofoveata) from all other mollusks as the most primitive molluscan

class on the basis of this homology is not upheld (see Salvini-Plawen, 1972a, paragraph 16).

In considering which character states of the alimentary tract may be primitive and which may be derived among the Aplacophora (Table 1), the following assumptions are made: (a) the Aplacophora are the sole living representatives of the primitive pre-placophorous mollusks and geologically very old (see Stasek, 1972; Salvini-Plawen, 1972a; Scheltema, 1978); (b) the least differentiated character state is usually the most primitive, unless there is some evidence for loss of structure; (c) a character state shared by most or all members is usually primitive, unless some evidence points to the contrary; (d) the radula capable of the least amount of manipulation is most primitive.

From the table certain relationships are clear (numbers below refer to character number in the table). The primitive character states held in common between the two subclasses are: cuticularization of the foregut (1); paired tubular salivary glands (lying ventrally both in *Scutopus megaradulatus* and in most Neomeniomorpha; perhaps secondarily lack-

TABLE 1. Primitive and derived character states of the aplacophoran alimentary tract (C = *Chaetoderma*, F = *Falcidens*, G = *Gymnomenia*, L = *Limifossor*, P = *Prochaetoderma*, S = *Scutopus*).

Character	Primitive	Derived (a, b, independently derived)
<u>Oral shield</u>		
(Neomeniomorpha not considered)	Entire S, F, C	Divided L, P
<u>Buccal cavity</u>		
1. Cuticle	Present G, S, L, P	Absent F, C
2. Goblet cells	Dominant G, S, L	Scattered P, F, C
3. Tubular salivary glands	One pair (most Neomeniomorpha) S, L, P	(a) Two pairs (F?), C (b) <sup>1</sup> Lacking G
4. Buccal sublingual pouch	Absent, or nearly so G, S	Present L, P, F, C
<u>Radula</u>		
5. Radular membrane	Divided or partially so, or line of fusion G, S, L	Entire P, (F?, C?)
6. Subradular membrane	Absent G, S	Present (L?), P, (F?, C?)

TABLE 1 (Continued).

Character	Primitive	Derived (a, b, independently derived)
7. Dentition	Distichous, without central plate G, S, L	(a) Distichous, with central plate P (b) Reduced F, C
8. Relationship of teeth to radular membrane	Not articulated G, S, L	(a) Articulated P (b) Reduced F, C
9. Bolster tissue	Connective tissue, muscle (G?), S, L, F, C	Chondroid-like P
10. Cuticular structure derived from odontophore	Absent G, S, L, F, C	Present P
11. Dorsal approximator of bolsters	Present (primitive?) S, L	Absent (derived?) G, P, F, C
<u>Esophagus</u>		
12. Length	Long, short S, L, C	(a) Extremely short P, F (b) Absent (derived?) G
13. Ciliation	Ciliated S, L	Not ciliated P, F, C
<u>Midgut</u>		
14. Ciliated dorsal band, groove, or typhlosole	Present (nearly all Neomeniomorpha) S, L, F, C	Absent (G?), P
15. Digestive diverticulum	Absent (primitive?) G (and all other Neomeniomorpha)	Present (derived?) S, L, P, F, C (and all other Chaetodermomorpha)
Chaetodermomorpha only:		
16. Dorsal granule cells, digestive diverticulum	Present S, L, F, C	Absent P
17. Lining of stomach	Not cuticular S, L, C	Cuticular (P?), F
18. Gastric shield	Absent S, L, P	Present F, C
19. Style sac	Absent S, L, P	Present F, C
20. Mucoid or protein rod(s)	Present throughout stomach and anterior intestine S	(a) Present, restricted location L, F, C (b) Absent P
<u>Feeding, diet</u>		
21. Feeding type	Detritivore-omnivore S, L, P	Selective carnivore G, F, C
22. Particle size	Dependent S, (L?) F, C	Independent (a) Suctorial G (b) Rasping P

<sup>1</sup>Considered primitive by Salvini-Plawen (1978).

ing in *Gymnomenia*) (3); a distichous radula lacking articulation (7, 8); a divided or fused radular membrane and lack of a subradular membrane (5, 6); and a ciliated dorsal band, groove, or typhlosole that runs the length of the midgut to a ciliated intestine (14). The foregut goblet cells (2) may not be homologous (cf. Figs. 3A, B, 4F).

The greatest difference between the two subclasses lies in the presence or absence of a digestive diverticulum (15). The undivided midgut of the Neomeniomorpha has been interpreted as primitive on the basis of (a) the lack of digestive adaptations (digestive gland, protostyle, gastric shield) for microphagous feeding (Salvini-Plawen, 1980) and (b) the presence of regular outpouchings caused by serially arranged dorso-ventral musculature (Boettger, 1956; Salvini-Plawen, 1969). (These outpouchings were first considered to be primitively lacking in *Genitoconia*, a member of the Wireniidae which includes *Gymnomenia* [Salvini-Plawen, 1967a], but later the lack of lateral pouches was considered to be secondarily derived [Salvini-Plawen, 1978]). Most neomeniomorphs have a very specialized cnidarian diet and thus the undivided midgut may be a specialized or reduced state, and not a primitive one. The single digestive diverticulum of the chaetoderms appears to have developed as a lobe from the stomach; it retains the evidence of its origin in the dorsal band of granular cells which can be traced forward to the stomach epithelium.

Among the Chaetodermomorpha there are two lines of evolutionary change from the least differentiated and therefore presumed primitive state found in *Scutopus*. One direction has been toward increased elaboration of the stomach into a posterior style sac, restriction of the protostyle to this sac, and increased cuticularization at the base of the stomach to form a gastric shield; morphoclines of these character states exist from *Scutopus* through *Limifossor* to *Falcidens* and *Chaetoderma* (Fig. 9). The other direction has been toward reduction as found in *Prochaetoderma*, with a single type of digestive cell in a shortened digestive diverticulum, no dorsal ciliated typhlosole, and no protostyle. The gastric shield is not correlated with general cuticularization of the stomach epithelium (Table 1: 17, 18). A convoluted intestine is found independently in the two genera that have long, thin "tails," *Prochaetoderma* and *Falcidens* (Fig. 1D, E).

The aplacophoran radula has evolved to-

wards freeing the teeth from their primitively broad attachment to the radular membrane and toward development of a sublingual pouch (4, 8). The result has been increased ability to manipulate or break down the food source.

In *Gymnomenia* the radula appears to be one of the most primitive among the Aplacophora (Fig. 4), but much work remains to be done on the diverse radular types found in other Neomeniomorpha (Nierstrasz, 1905; Salvini-Plawen, 1967b, 1978). Among cnidarian feeders with a suctorial foregut, reduction and specialization could be expected; nevertheless, a primitive type of radula occurs in carnivores in the Aplacophora.

The radulae among chaetoderm genera differ greatly in morphology and cannot readily be derived from a primitive type or from each other except in terms of function. Primitively, teeth are affixed to the radular membrane and the odontophore is scarcely free in the buccal cavity; only a sliding motion combined with closing opposed teeth is possible (*Scutopus*, Fig. 5). More complicated movements can occur in *Limifossor* with a split radular membrane and a relatively enormous odontophore (Figs. 1C, 6B; Heath, 1905). A rasping gastropod-like radula has evolved only in *Prochaetoderma* (Fig. 7). The reduced, highly modified radula of *Falcidens* and *Chaetoderma* is probably capable of precise movement in prey capture (Ivanov, 1979). The two most highly evolved radulae occur in the two groups which are carnivorous or carnivorous-omnivorous and which also have the most modified midguts: *Prochaetoderma* with the most complex radula and most reduced midgut and the Chaetodermatidae (*Falcidens* and *Chaetoderma*) with the most modified radula and most complex midgut. There does not appear to be a morphocline in radula type in the Chaetodermomorpha (see Salvini-Plawen, 1975).

#### Phylogenetic Considerations: Interclass

The style sac and gastric shield are shown by the Aplacophora to have evolved more than once in the Mollusca. In the Aplacophora, a protostyle has evolved before a style sac, and a style sac and gastric shield occur only in a carnivorous family (Chaetodermatidae).

A radula capable of rasping seems to require a single radular membrane, a subradular membrane, a bending plane, firm bolsters,

and some way for the teeth to articulate on the radular membrane. There also must be some way to keep the mouth open during rasping. In gastropods the mouth opens as part of radula protraction (Graham, 1973), but in *Prochaetoderma*, which uses its head for locomotion (burrowing) as well as for feeding, unique jaws have evolved which can keep the mouth open during rasping. The significance of rasping as a feeding mechanism is that feeding is not particle-size dependent (Table 1: 22); large pieces of food can be broken down and manipulated before ingestion, whether the food be a large algal mat on a hard surface, prey, or large pieces of detritus. The ability to manipulate food before ingestion may be one of the reasons for the great success of the gastropods.

It is not possible on the evidence presented here to determine the structure of the archimolluscan alimentary tract. Certainly it had a nonarticulated radula with protractors, retractors, and bolsters, paired tubular salivary glands, a cuticular foregut, and a dorsal ciliated tract running down the midgut. If the Neomeniomorpha have retained a primitive midgut even though they have become food specialists, then a digestive gland must have been derived more than once in the mollusks. On the other hand, if the neomeniomorph midgut is reduced, then a protostyle without a style sac or gastric shield and a digestive diverticulum could have been primitively present in the mollusks, a condition that would lead more directly to parallel evolution in the molluscan midgut of a style sac and gastric shield. The two studies on aplacophoran gut development for two Neomeniomorpha did not have this question in mind (Baba, 1938; Thompson, 1960), but Baba observed that the intestine arises from endoderm and that the midgut epithelium when it first forms is thickest laterally and ventrally, as it is in the chaetoderm digestive diverticulum.

The evidence from entire, isolated radulae of Aplacophora indicates for the mollusks an original state of distichous rows of teeth on a divided radular membrane. The evidence for an original single basal membrane with rows of broad monoserial teeth rests on reconstructions from histologic sections of the neomeniomorph radula of *Dondersia* (Nierstrasz, 1905), on histologic sections of *Simrothiella* (Salvini-Plawen, 1972a), and on ontogenetic studies on chitons (Minichev & Sirenko, 1974). Kerth (1979) has shown, on the other hand, that distichous teeth on a sin-

gle membrane develop ontogenetically in the pulmonates.

The questions of whether the archimolluscan radula was a single or paired structure and whether or not the midgut had a digestive diverticulum is left open for further observations on isolated aplacophoran radulae, comparative histologic studies and studies on development.

#### Ecological Considerations

Although Aplacophora are ubiquitous in the deep sea from the edge of the continental shelf to the deepest abysses and hadal depths, they seldom are numerically an important constituent of the macrofauna. The two chaetoderm genera described here which are the most primitive also have the fewest known species: *Scutopus* (4) and *Limifossor* (4). The number may be doubled, at most, from existing collections not yet described. The carnivorous species belonging to *Falcidens* and *Chaetoderma* are far more numerous, although their total numbers in any one sample are never great (unpublished data).

Species of *Prochaetoderma* are numerous (unpublished data) and can be the numerically dominant macrofaunal animals in quantitative samples. *Prochaetoderma* sp. y was the dominant species in a total of twenty-five 35-cm<sup>2</sup> tubular cores taken at one 1,760-m station off Woods Hole (Grassle, 1977), although dominance was not high (6.0%; discrepancy from Grassle's data due to recent recognition of a sibling species). The next four most numerous species were polychaete worms (5.1%, 4.4%, 4.2%, and 3.7%) (nematodes, ostracods, and copepods excluded). Actual density of *Prochaetoderma* y was 309 m<sup>-2</sup>. In a ¼-m<sup>2</sup> spade box core taken in the same area, this species was the fourth most numerous species with a density of 192 m<sup>-2</sup>. In other quantitative samples in the same area, *Prochaetoderma* y ranged in numbers up to 237 m<sup>-2</sup>, and in grab samples taken between 1141 and 2148 m depths it ranged up to 400 m<sup>-2</sup>.

In a ¼-m<sup>2</sup> spade box core taken in the remarkably productive Aleutian Trench off Alaska at a depth of 7298 m, another *Prochaetoderma* was one of the dominant species at a density of 124 m<sup>-2</sup> (Jumars & Hessler, 1976).

The numerical success of some species of *Prochaetoderma* may be attributable in part

to their efficient gastropod-like rasping radula, which has made a wide size range of food sources available to them in an environment where food is probably a limiting factor.

### CONCLUSION

The Aplacophora exhibit a wide variation in morphology of the alimentary tract. Comparative studies of these morphologies give insight into evolutionary events and function among the Mollusca and lead to a greater understanding of feeding in the deep sea.

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### LITERATURE CITED

- BABA, K., 1938, The later development of a solenogastre, *Epimenia verrucosa* (Nierstrasz). *Journal of the Department of Agriculture, Kyushu University*, 6: 21-40.
- BABA, K., 1939, Preliminary note on *Epimenia verrucosa* (Nierst.). *Venus*, 9: 35-42 (in Japanese).
- BABA, K., 1940, *Epimenia ohshimai*, a new solenogastre species from Amakusa, Japan. *Venus*, 10: 91-96 (in Japanese).
- BOETTGER, C. R., 1956, Beiträge zur Systematik der Urmollusken (Amphineura). *Zoologischer Anzeiger*, Suppl. 19: 223-256.
- FRETTER, V. & GRAHAM, A., 1962, *British prosobranch molluscs*. Ray Society, London, 755 p.
- GRAHAM, A., 1973, The anatomical basis of function in the buccal mass of prosobranch and amphineuran molluscs. *Journal of the Zoological Society of London*, 169: 317-348.
- GRASSLE, J. F., 1977, Slow recolonisation of deep sea sediment. *Nature*, 265: 618-619.
- HEATH, H., 1905, The morphology of a solenogastre. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, 21: 703-734, pl. 42-43.
- HOFFMAN, S., 1949, Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. *Zoologiska Bidrag från Uppsala*, 27: 293-427.
- IVANOV, D. L., 1979, Structure and functional morphology of the radular system in *Chaetoderma* (Mollusca, Caudofoveata). *Zoologicheskii Zhurnal*, 58: 1302-1306 (in Russian).
- JUMARS, P. A. & HESSLER, R. R., 1976, Hadal community structure: implications from the Aleutian Trench. *Journal of Marine Research*, 34: 547-560.
- KERTH, K., 1979, Phylogenetische Aspekte der Radulamorphogenese von Gastropoden. *Malacologia*, 19: 103-108.
- KOWALEVSKY, A., 1901, Sur le genre *Chaetoderma*. *Archives de Zoologie expérimentale et général*, sér. 3, 9: 261-284, pl. 10-12.
- MINICHEV, A. S. & SIRENKO, B. J., 1974, Development and evolution of the radula in Polyplacophora. *Zoologicheskii Zhurnal*, 53: 1133-1139 (in Russian).
- NIERSTRASZ, H. F., 1903, Neue Solenogastren. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, 18: 359-386, pl. 35-36.
- NIERSTRASZ, H. F., 1905, *Kruppomenia minima* und die Radula der Solenogastren. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, 21: 665-702, pl. 39-41.
- ODHNER, N. H., 1921, Norwegian Solenogastres. *Bergens Museums Aarbok 1918-1919*, Nr. 3, 1-86, pl. 1-6.
- PRUVOT, G., 1891, Sur l'organisation de quelques néoméniens des côtes de France. *Archives de Zoologie expérimentale et général*, sér. 2, 9: 699-806, pl. 25-31.
- SALVINI-PLAWEN, L. V., 1967a, Neue scandinavische Aplacophora (Mollusca, Aculifera). *Sarsia*, 27: 1-63.
- SALVINI-PLAWEN, L. V., 1967b, Über die Beziehungen zwischen den Merkmalen von Standort, Nahrung und Verdauungstrakt bei Solenogastres (Aculifera, Aplacophora). *Zeitschrift für Morphologie und Ökologie der Tiere*, 59: 318-340.
- SALVINI-PLAWEN, L. V., 1969, Solenogastres und Caudofoveata (Mollusca, Aculifera): Organisation und phylogenetische Bedeutung. *Malacologia*, 9: 191-216.
- SALVINI-PLAWEN, L. V., 1972a, Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Zeitschrift für wissenschaftliche Zoologie*, 184: 305-394.

- SALVINI-PLAWEN, L. V., 1972b, Die Caudofoveata des Mittelmeeres und das Genus *Scutopus* (Mollusca, Aculifera). In *Fifth European Marine Biology Symposium*, Battaglia, B. (ed.) Piccin, Padua, p. 27-51.
- SALVINI-PLAWEN, L. V., 1975, Mollusca Caudofoveata. *Marine Invertebrates of Scandinavia* 4, Universitetsforlaget, Oslo, 55 p.
- SALVINI-PLAWEN, L. V., 1978, Antarktische und subantarktische Solenogastres (eine Monographie: 1898-1974). *Zoologica* (Stuttgart), 44: 1-315.
- SALVINI-PLAWEN, L. V., 1980, Molluscan digestive system in evolution. *Haliotis*, 10(2): 127 [abstract].
- SALVINI-PLAWEN, L. V., in press? Diets for aplacophoran and monoplacophoran molluscs. *Handbook of Nutrition and Food*, CPC Press.
- SALVINI-PLAWEN, L. V. & NOPP, H., 1974, Chitin bei Caudofoveata (Mollusca) und die Ableitung ihres Radulaapparates. *Zeitschrift für Morphologie der Tiere*, 77: 77-86.
- SCHELTEMA, A. H., 1972, The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere*, 72: 361-370.
- SCHELTEMA, A. H., 1973, Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere*, 76: 97-107.
- SCHELTEMA, A. H., 1976, Two new species of *Chaetoderma* from off West Africa (Aplacophora, Chaetodermatidae). *Journal of Molluscan Studies*, 42: 223-234.
- SCHELTEMA, A. H., 1978, Position of the class Aplacophora in the phylum Mollusca. *Malacologia*, 17: 99-109.
- SCHWABL, M., 1961, *Crystallophrisson* (= *Cybaetoderma*) *hartmani* nov. spec., eine neue Aplacophore aus dem Östpazifik. *Zoologischer Anzeiger*, 166: 258-277.
- SCHWABL, M., 1963, Solenogaster mollusks from southern California. *Pacific Science*, 17: 261-281.
- STASEK, C. R., 1972, The molluscan framework. In *Chemical Zoology*, VII. *Mollusca*, FLORKIN, M. & SCHEER, B. T. (eds.), p. 1-44.
- THOMPSON, T. E., 1960, The development of *Neomenia carinata* Tulberg (Mollusca Aplacophora). *Proceedings of the Royal Society of London*, ser. B, 153: 263-278.
- WIRÉN, A., 1892, Studien über die Solenogastres. I. Monographie des *Chaetoderma nitidulum* Lovén. *Kongliga Svenska Vetenskaps-Academiens Handlingar*, 24(12): 66 p., 7 pl.





## TWO NEW SPECIES OF *CHAETODERMA* FROM OFF WEST AFRICA (APLACOPHORA, CHAETODERMATIDAE).<sup>1</sup>

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### INTRODUCTION

Species descriptions of aplacophoran mollusks have been based in large part on internal anatomy as understood from histological preparations. The results, as important as they may be in understanding anatomical and phylogenetic relationships among the Aplacophora, do not lend themselves to quantitative studies of populations nor to ease in identifying a specimen in hand. Histological preparations are not only time-consuming to make, they also destroy the specimen and are particularly prone to error in interpretation (e.g., Scheltema, 1973, on the anatomy of the heart and pericardium of *Chaetoderma nitidulum*). Hard parts — spicules and radula — have seldom been illustrated in sufficient detail for positive identifications.

It has been my purpose to find morphological characters useful both for population studies and for species identification. The descriptions given here for two new species, represented by only two individuals each, of necessity are concerned with identification; however, the characters used to describe them result from analyses (unpublished) of intraspecific variation in several populations of the relatively common species *Chaetoderma nitidulum* Lovén. Some of these characters are applied for the first time to aplacophoran taxonomy; some, used by previous authors, are examined and described in greater detail. The characters are as follows:

- (1) Body morphology: (a) dimensions of definable body regions and their ratios, (b) shape of the oral shield, (c) shape and spiculation of the mantle cavity, and (d) size of the dorsoterminal sensory organ.
- (2) Spicule morphology: as observed with both scanning electron and light microscopy.
- (3) Radula morphology: dimensions of discrete structures and their ratios.

### *Body morphology*

Many species of *Chaetoderma* exhibit four distinct, measurable body regions (Fig. 2, lower right): *A*, cephalic region lying in front of the anterior constriction but not including the cephalic lobe, which may or may not be protruded; *B*, region of heavy longitudinal muscle bands within which lies the stomach; *C*, region of gonad and digestive gland; and *D*, region of the mantle cavity. Statistical analyses of the measurements of these body regions in *C. nitidulum* showed that on the average for contracted, preserved specimens there is a constant relationship between the length of each region and

<sup>1</sup> Contribution No. 3520 from the Woods Hole Oceanographic Institution.

total body length  $E$ , and between the diameters of regions  $B$  and  $C$  and total length  $E$ . The external shape reflects the organization of internal organs, which are held in place by muscle fibres running between them and the body wall. The nomenclature of Wirén (1892) for these four regions — prothorax, metathorax, preabdomen, and postabdomen — is discontinued as it is anatomically without meaning (Hyman, 1967) and does not have a universal application to all chaetodermatid shapes.

The oral shield ('Fusschild' of Salvini-Plawen, 1968), dorsoterminal sensory organ, and mantle, or cloaca, are here described qualitatively only.

#### Spicule morphology

The spicules of the Aplacophora are ornamented to varying degrees. In the family Chaetodermatidae they generally lie tangential to the body wall and are overlapped, with the distal, pointed ends directed posteriorly, or, in particular regions of some species, they are bent at their proximal ends and held erect, perpendicular to the contracted body wall. Ornamentation is on the outer side; if the inner side is grooved, the base of the spicule appears indented. (Figs 1, 2). The spicules very often have a median keel. They differ

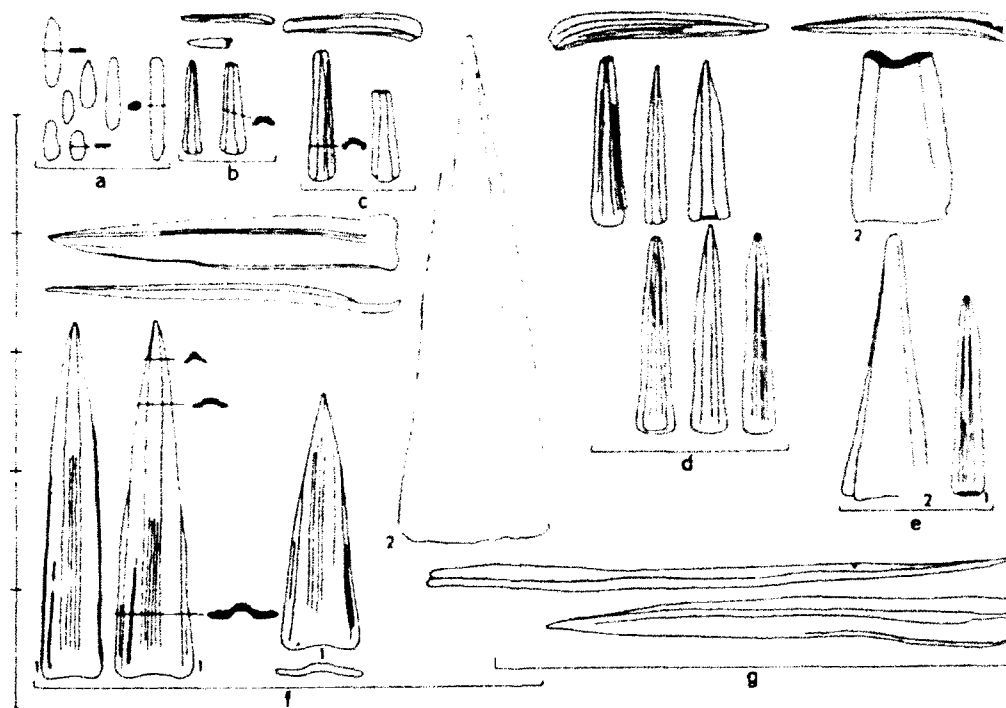


Fig. 1. *Chaetoderma abidjanense* n. sp. Spicules from areas a-g, indicated on outline drawing. Fig. 2. lower left. Cross-sections black, inner sides stippled, ridges indicated by single line. Lateral views horizontal. Each division on vertical scale = 100 µm. e: Type 1 spicule on left, type 2 on right; cf. Pl. 1a-c, f, f: Three type 1 spicules on left, type 2 on right.

morphologically along the body from anterior to posterior, and any part of the body may bear more than one type of spicule. Within a species the predominance of type can change with age. Dorsal and ventral spicules have been examined by scanning electron microscope from the same body area in one specimen of *C. nitidulum*; they were morphologically the same, and it is assumed here that spicules in all species of

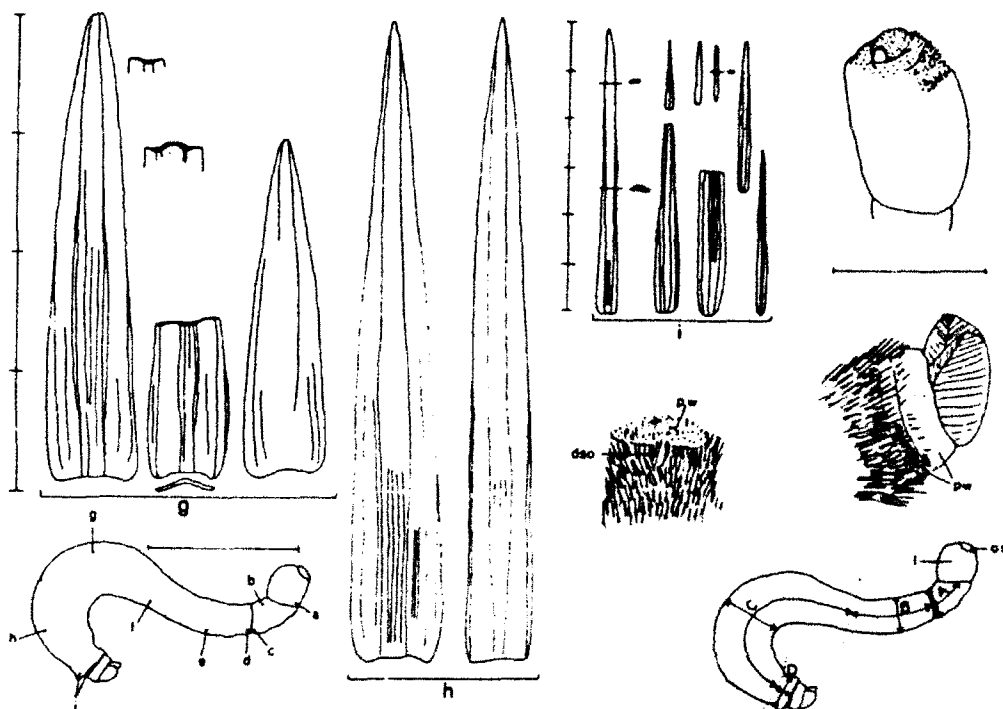


Fig. 2. *Chaetoderma abidjanense* n. sp. Spicules from areas g-i; devices and vertical scales as in Fig. 1. g: Two type 1 spicules on left, type 2 on right; lateral views in Fig. 1; cf. Pl. 1d, e, g, h. h: Type 1 spicule on left, type 3 on right, type 2 not illustrated. i: Note reduced scale. Lower left and right, paratype (USNM 760630) showing regions from which spicules were taken (a-h) and body regions measured (A-D). Upper right, anterior end of holotype. Center right, mantle and gills of holotype and paratype. Horizontal scales: for paratype, 8 mm; for anterior and posterior ends, 2 mm. dso dorsoterminal sensory organ, l cephalic lobe, os oral shield, pw posterior wall of mantle.

*Chaetoderma* do not differ on dorsal and ventral sides.

With the aid of scanning electron microscope the detailed ornamentation and structure of the spicules appear, so that spicule images seen in the light microscope can be interpreted (cf. Plates 1, 2 and Figs 1, 2, 4, 5). Without the SEM, it is virtually impossible to understand light microscope images.

#### *Radula morphology*

The radula is at present the definitive character of the family Chaetodermatidae and is used to distinguish the only two genera, *Falcidens* and *Chaetoderma* (Salvini-Plawen, 1968). In the genus *Chaetoderma* it has been described (Scheltema, 1972) as consisting of a cone-shaped structure (*i*) with paired, thin, lateral projections (*p*) which are connected to a dome-shaped membrane (*s*) thickened laterally (Fig. 3); the lateral projections lie opposite a pair of denticles (*d*). The cone-shaped structure has been interpreted as a fused radula (Scheltema, 1972) or as a greatly thickened basal membrane (Boettger, 1955; Schwabl, 1961; Salvini-Plawen, 1974), and the dome-shaped membrane as a subradular membrane, or not so. In *C. nitidulum* the cone-shaped structure *i* and membrane *s* increase in length with increase in body length. However, the denticles *d* and lateral projections *p* maintain a nearly constant length and are not correlated to body length.

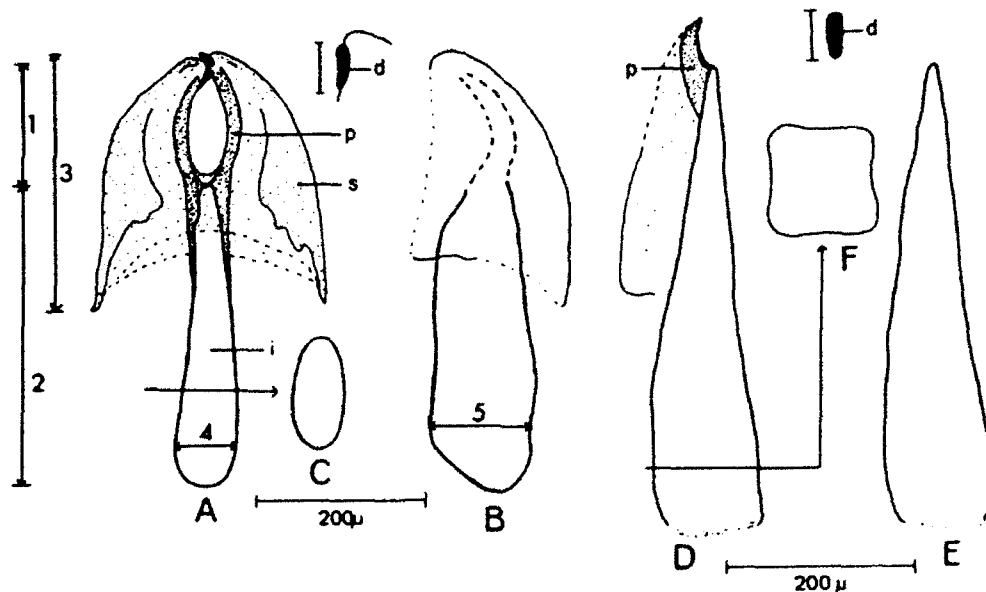


Fig. 3. Radulae of *Chaetoderma abidjanense* n. sp. (A-C) (paratype, USNM 760630) and *C. majusculum* n. sp. (D-F) (paratype, USNM 760633). Dimensions determined: (1) length of lateral projection *p*, (2) length of cone *i*, (3) length of subradular membrane *s*, (4) frontal width of cone *i*, (5) lateral width of cone *i*, and (6) length of denticle *d*. (A, D) frontal views, (B, E) lateral views, (C, F) semi-schematic cross-sections of cone *i*. Horizontal scales = 200  $\mu$ m; vertical scales for denticles = 25  $\mu$ m.

Six dimensions were found to be taxonomically useful (Fig. 3): (1) distance from tip of cone *i* to tip of denticle *d*, giving a measure of lateral projection *p*; (2) length of cone *i*; (3) length of membrane *s*; (4) greatest frontal width of cone *i*; (5) greatest lateral width of cone *i*; and (6) length of denticle *d*. From these dimensions three ratios were derived: (1) length of membrane *s* to length of cone *i*, (2) frontal width to lateral width of cone *i*, and (3) length of cone *i* to total body length *E*. Although the last ratio increases in *C. nitidulum* with increasing body length, the rate of increase differs for different geographic populations.

#### METHODS

Body dimensions were measured with dividers set to a stage-micrometer scale on camera-lucida outline drawings of entire animals. Lengths were taken along the midline and the diameters of each body region were measured as shown in Fig. 2.

Radulae were dissected, treated, and drawn as previously described (Scheltema, 1972). Measurements were made as shown in Fig. 3 using dividers on camera-lucida drawings.

Spicules were removed with the point of a sharp dissecting blade. For light microscopy they were placed in glycerol in a depression slide and drawings made by means of a camera lucida. Care was taken to draw spicules lying in a horizontal plane with all edges in focus at once. For examination with a scanning electron microscope, spicules were washed by agitating them in distilled water in a deep depression dish and transferred in a drop of water to coverslip glass glued to a brass SEM stud. After drying overnight in a desiccator, the spicules were coated with gold.

## DESCRIPTION

Genus *Chaetoderma* Lovén, 1844 (type, by monotypy, *C. nitidulum* Lovén) [nom. conserv., ICZN, 1966, No. 764] [= *Crystallophrisson* Möbius, 1874]

*Chaetoderma abidjanense* n. sp. (Pl. 1, Figs 1,2,3, Tables 1,2).

*Material*

2 entire specimens, 1 fragment.

Holotype: off Ivory Coast 5°10.3' N, 4°05'W. 80 m. Sand with 57% <50µm. CRO Station 5, 23/XI/66. USNM 760629.

Paratype, radula removed: 5°02.5'N, 3°47'W. 80 m. 80% sediment <50 µm. CRO Station 2, 18/VIII/66. USNM 760630.

Fragment (posterior): 5°12'N, 4°02'W. 80 m. Sediment oolitic, 43% <50 µm. CRO Station 3, 22/XI/66. USNM 760631.

*Diagnosis*

Total body length (2 specimens) about 18 mm; stout, greatest diameter about 3 mm; length and diameter of stomach region distinct, 1/4 and 1/10 total length, respectively; digestive-gland region twice as long and wide as stomach region; mantle short, less than 2/3 diameter, and straight-sided with short fringing spicules; dorsoterminal sensory organ short and distinct; shape of small oral shield not known. Spicules heavily ridged longitudinally with pronounced keel, grooved on inner side, proximal end indented. In stomach region spicules 30 x 200 µm; held erect; proximal end bent outward at 30° angle: outer side with broad, platform-like keel bearing 0-3 ridges; lateral edges thick, rounded, and ridged; inner side deeply grooved. In digestive-gland region spicules 70-80 x 300-400 µm; keel wide, appearing rounded under SEM but flat under light microscope, broadest centrally, with 0 to several ridges running part way to tip, broad central portion with most ridges; groove on either side of keel with one or several ridges running 1/3 distance to tip; distinct lateral ridge parallel to each edge running 1/2 distance to tip, 0-2 ridges between lateral ridge and spicule edge; inner side grooved and with a single ridge. Radula cone (1 specimen) 350 µm long, frontal width narrow (75 µm), lateral width 1-2/3 times frontal width, lateral projections long (140 µm), length of subradular membrane more than 4/5 cone length.

*Description*

Body morphology (refer to Table 1): stout, large, four body regions distinct (Pl. 1, Fig. 2). Oral shield small (os, Fig. 2), shape not known. Spicules perpendicular to body wall in region B, sediment packed between them; in region C, spicules flat-lying. Mantle region D straight-sided both with gills extended and retracted (Fig. 2); spicules thickly spaced and scarcely extending beyond end of mantle; posterior wall (pw) of closed cloaca flat, spicules with brown encrustations; gills large; dorsoterminal sensory organ (dso) small but distinct.

Spicule morphology (Pl. 1, Figs 1,2): From cephalic lobe *area a*: thin or thick; distal end blunt or pointed; no ornamentation. From remainder of body (*b-i*) outer side with broad median keel, which changes along body from steep-sided anteriorly to rounded posteriorly, usually with several sharp longitudinal ridges; inner side of spicules grooved; anterior spicules with proximal end bent acutely toward outer side. *Area b*: thick; some as in *area a*; most with raised, somewhat concave, platform-like keel

TABLE 1

Lengths and diameters of body regions and their ratios in *Chaetoderma abidjanense* and *C. majusculum* (refer to Fig. 2 for letter designations).

Species and location		Lengths (l) and diameters (d) (mm)								Length : 1 <sub>E</sub>				d : 1 <sub>E</sub>			
		A		B		C		D		Total E	A	B	C	D	B	C	
		Body region	1	d	1	d	1	d	1								d
<i>C. abidjanense</i>																	
CRO Sta. 5 (holotype)		2.3	1.3	4.8	1.5	10.2	2.6	1.0	1.6	18.4	.13	.26	.55	.05	.08	.14	
CRO Sta. 2 (paratype)		2.1	1.7	4.6	2.0	10.9	3.4	1.0	1.8	18.7	.11	.25	.58	.05	.11	.18	
Mean		—	—	—	—	—	—	—	—	—	.12	.26	.57	.05	.10	.16	
<i>C. majusculum</i>																	
Trou sans fond (holotype)		4.1	2.0	9.7	2.0	24.4	2.8	1.7	3.0	40.0	.10	.24	.61	.04	.06	.07	
CRO Sta. 4 (paratype)		(Stretched)				22	3.2	1.5	3.0	—	—	—	—	—	—	—	

lacking ridges. *Area c*: thick; keel steep-sided, platform-like, ridged or lacking ridges; edges of spicules rounded. *Area d*: thick; keel narrow to broad, platform-like, with 0-3 ridges; edges thick and rounded with longitudinal ridges; inner side deeply grooved; proximal end bent outward at about 30° and slightly flared; distal end pointed. *Area e*: two types; type 1 dominant, like spicules in area *d*; type 2 longer and wider, thick, with very broad median platform without ridges, or ridges very faint. *Area f*: two types; type 1 thinner, flatter than type 1 spicules in more anterior areas; keel broad, flat, bearing 2-4 ridges from 20 µm above base of spicule to 1/2-5/6 total length; flat area on either side of keel with or without short ridges; edges, with 0-2 ridges, sloped and running 1/2-2/3 length of spicule; proximal end slightly flared, slightly bent, and indented at base; type 2 spicules like type 2 in area *e* but larger. *Area g*: two types; type 1 dominant, long, bent towards inner side 1/3 distance from base; keel rounded with 3 or more ridges running 1/2 spicule length, broadened centrally with additional ridges; grooves with 1-3 ridges on each side of keel; edges as in spicule type 1 of area *f*; inner side of spicule thickened on either side of medial groove bearing single median ridge (Pl. 1g); proximal end indented, not flared; type 2 short, keel very broad, rounded, lacking ridges; grooves on each side of keel ridged; edges without ridges. *Area h*: three types; type 1 similar to type 1 spicules of area *g* except longer, ridges of keel only 1/3 spicule length, and grooves on each side of keel deeper; type 2 like type 2 of area *g*; type 3 similar in shape to type 1 but with ridges very faint. *Area i*: several types, most with a keel or median ridge; longest spicules with slight groove on inner side, and with keel narrow, ridged or only faintly so, forming most of spicule width; spicules of intermediate length very narrow with narrow keel lacking ridges, shortest spicules pointed or blunt distally, with or without central ridge.

Radula morphology is summarized in Figure 3 and Table 2.

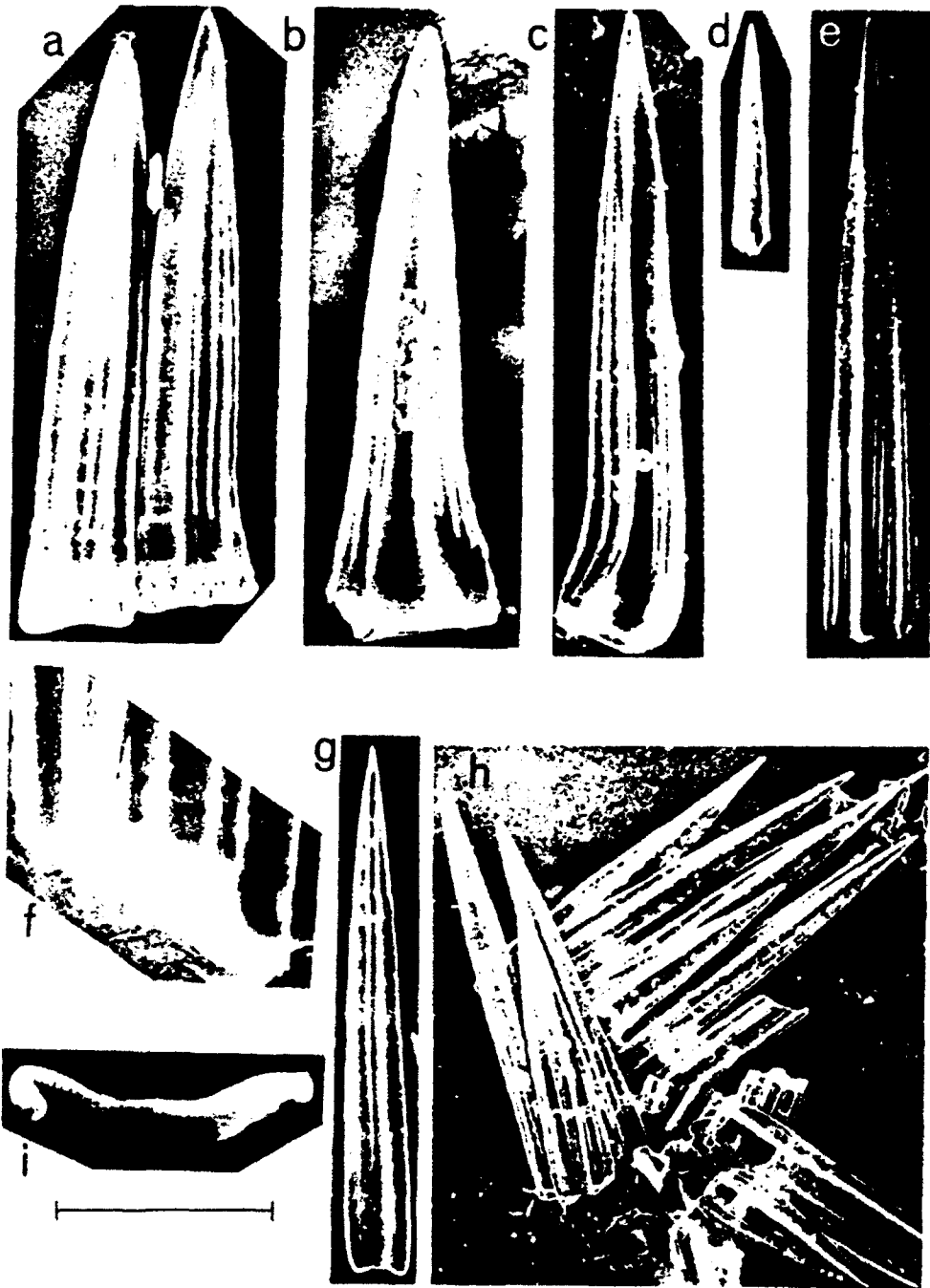


Plate 1. *Chaetoderma abidjanense* n. sp. (a-h) Scanning electron photomicrographs of spicules from paratype (USNM 760630); (i) holotype (USNM 760629), scale = 10 mm. (a, b, c, f) Spicules from area e (see Figs. 1, 2): (a) outer side; (b) inner side; (c) lateral view, inner side facing to right; (f) detail of broad, ridged, platform-like keel; taken at 600X, 600X, 550X and 2,000X, respectively. (d, e, g, h) Spicules from area h (see Fig. 2): (d) tip of outer side showing broadening of rounded keel and narrow edges; (e) outer side of type 1 spicule; (g) inner side; (h) group of type 1 spicules, one type 2 spicule at lower right; taken at 160X, 180X, 160X, and 140X, respectively.

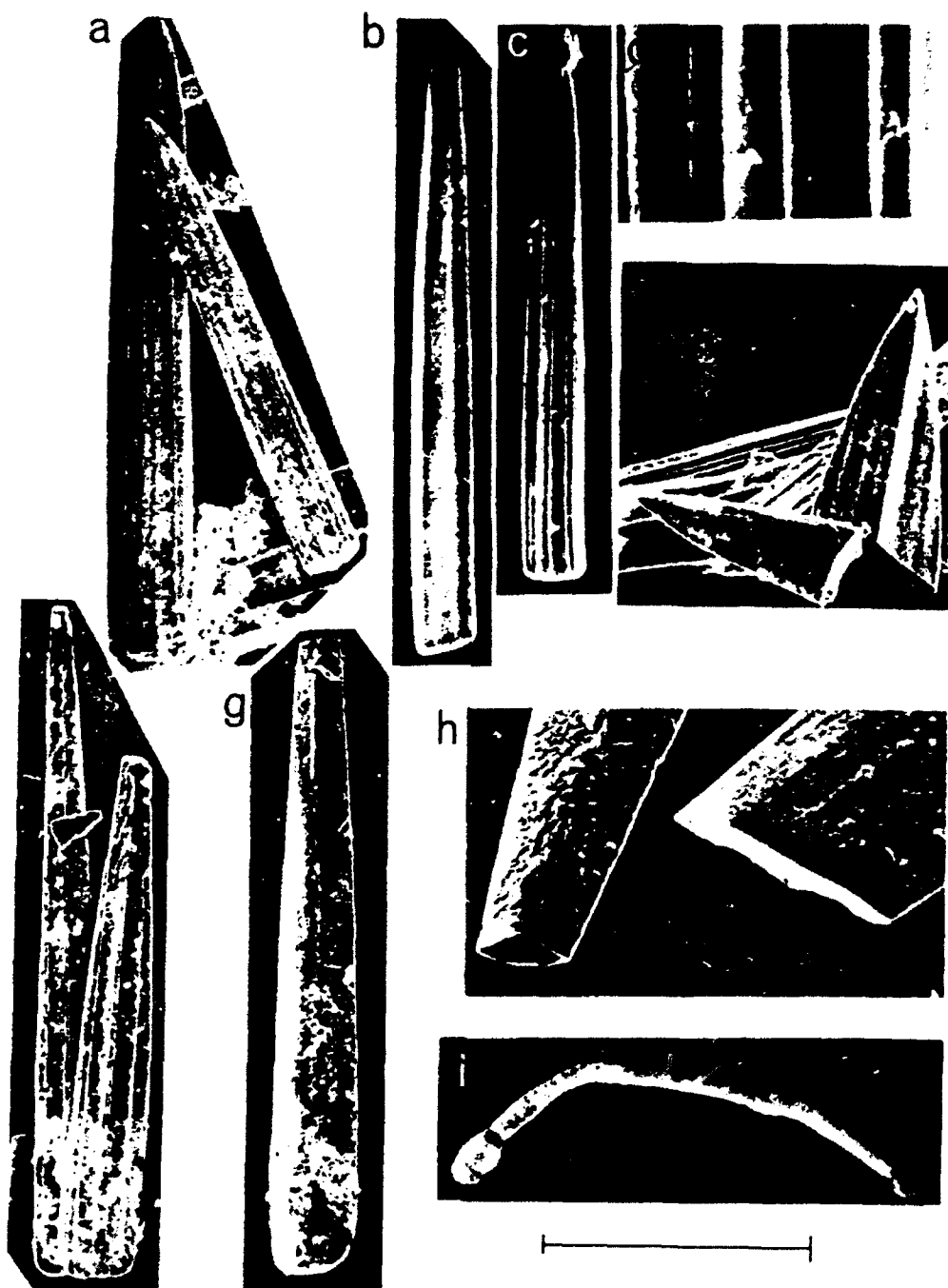


Plate 2. *Chaetoderma majusculum* n. sp. (a-h) Scanning electron photomicrographs of spicules taken from holotype (USNM 760632), (i) holotype, scale = 20 mm. (a-e) Spicules from areas b and c (see Figs. 4,5): (a) outer side of type 1 spicule, area b; (b) inner side, area c; (c, d) outer side and detail, area c; (e) cross-sections area b, outer side facing upwards, showing groove and ridges of inner side, distal end of type 1 spicule to left, type 3 to right; taken at 250X, 300X, 180X, 1,000X, and 500X, respectively. (f-h) Spicules from area f (see Fig. 5): (f) outer side of type 1 and 3 spicules; (g) outer side of type 2 spicule; (h) left: outer side of type 2 spicule, cross-section of tip; right, inner side and cross-section of type 1 spicule; taken at 140X, 180X, and 600X, respectively.



*Chaetoderma majusculum* n. sp. (Pl. 2, Figs 3, 4, 5 Tables 1, 2).

#### Materials

2 entire specimens, one distorted by stretching.

Holotype: off Ivory Coast 5°12'N, 3°58'W. 200-300 m. CRO Station "E. Trou sans fond", 13/XI/66. USNM 760632.

Paratype, radula removed: 5°09.5'N, 4°02'W. 100 m. Fine sediment, 90% < 50 µm. CRO Station 4, 22/XI/66. USNM 760633.

#### Diagnosis

Large, total body length (1 specimen) 40 mm, and stout, greatest diameter 3 mm; division between stomach and digestive gland regions not distinct; length and diameter of stomach region 1/4 and 1/20 total length, respectively; digestive gland region 2½ times longer than stomach region and not quite 1½ times wider; mantle short, length ½ diameter, rounded, with flat-lying, truncated spicules; dorsoterminal sensory organ small and indistinct; oral shield large, entirely surrounding mouth opening. Spicules long, straight, flat, and ridged, proximal end scarcely bent, median keel not pronounced except distally, 1-4 medial ridges, 2 or more lateral ridges, proximal end rounded. In stomach region spicules 40-60 x 200-400 µm, flat-lying, single median ridge running from base to tip, 2 lateral ridges running 4/5 distance to tip; inner side with shallow median groove, thickened laterally. In digestive-gland mid-region, spicules 30-60 x 300-500 µm; 1-2 medial and 1-2 lateral ridges run from base ½ or more distance to tip, slightly grooved and not ridged between medial and lateral ridges, tip triangular with central keel. Radula cone large, 600 µm long and 130 µm wide frontally and laterally, lateral projections 65 µm, length of subradular membrane 3/5 cone length.

#### Description

Body morphology (refer to Table 1): Large, anterior constriction and mantle distinct but not division between stomach and digestive gland (Pl. 2, Fig. 5). Oral shield large, entire, pierced by mouth opening (Fig. 4). Spicules in regions B and C flat-lying. Mantle region D rounded and button-like, with short, truncated, flat-lying spicules (Fig. 4); size of gills not known; indistinct dorsoterminal sensory organ small.

Spicule morphology (Pl. 2, Figs. 4, 5): No spicules preserved on cephalic lobe or body region A. From remainder of body (areas a-h) spicules long, with medial and lateral ridges, flat or slightly grooved, and scarcely or not bent; bases straight or rounded. *Area a*: two broad ridges on outer side, somewhat bent outward at extreme proximal end, inner side grooved. *Area b*: three types; type 1 with single narrow medial ridge extending length of spicule, lateral ridges extending about 4/5 length of spicule; distal end keeled; inner side with a lateral ridge on each side of shallow groove; bent outward at proximal end less than 5°; type 2 with broad, flattened median platform-like keel not running full length of spicule; type 3 (Pl. 2e) like those of type 2 in area e. *Area c*: two types; type 1 like type 1 spicules of area b but with wide range in size; type 2 (not figured) like type 2 spicules in area e. *Area d*: spicules poorly preserved, probably like those from areas b and c; not bent proximally. *Area e*: three types, not bent proximally; type 1 with one or more medial ridges, one running length of spicule, and 1-3 lateral ridges set off from medial ridges by shallow groove; inner side with shallow groove proximally, rounded distally; type 2 with ridges faint except single median ridge running length of spicule; inner side not rounded distally; type 3 short and rounded, lacking ridges but keeled distally. *Area f*:

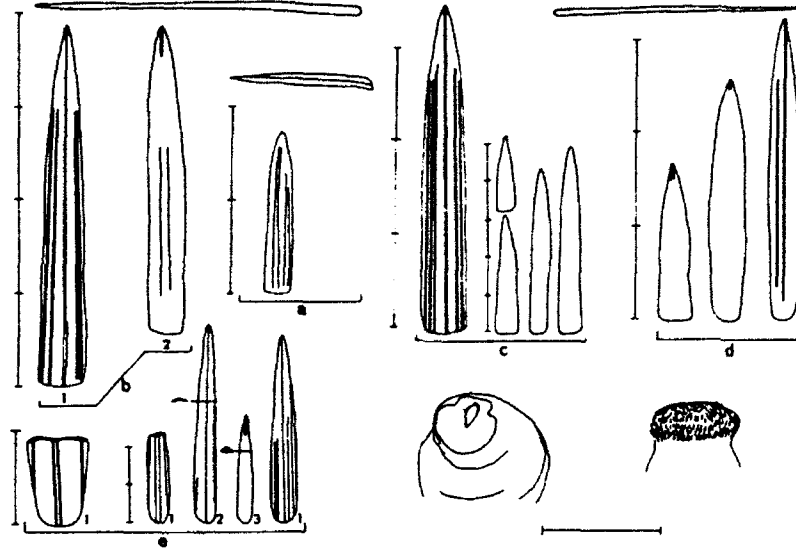


Fig. 4. *Chaetoderma majusculum* n. sp. Spicules from areas a-e indicated on outline drawing, Fig. 5; each division on vertical scales = 100  $\mu$ m and apply to those spicules lying to the right of them; ridges indicated by double lines on large-scale drawings, by single lines on small-scale drawings; other devices as in Fig. 1. b: Type 1 spicule on left, type 2 on right, type 3 not illustrated; cf. Pl. 2a, e. c: Type 1 spicules only, type 2 not illustrated; large-scale drawing shows ridges, small-scale drawings show size range, ridges not indicated; cf. Pl. 2b, c, d. e: Type 1 spicule left, at large scale; at small scale, type 1 left and right, type 2 second from left, type 3 second from right. Lower right: oral shield and mantle of paratype (USNM 760633), scale = 2 mm for shield, 4 mm for mantle.

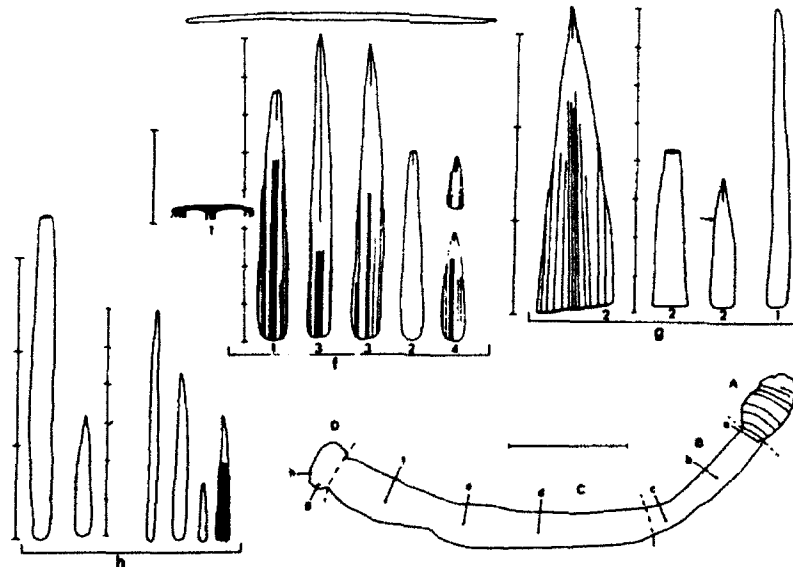


Fig. 5. *Chaetoderma majusculum* n. sp. Spicules from areas f-h; vertical scales and ridges as in Fig. 4. f: Cross-section of type 1 spicule at large scale; at small scale, type 1 at left, type 2 second from right, type 3 second and third from left, type 4 far right; cf. Pl. 2f, g, h. g: Type 1 spicule at far right; three type 2 spicules at left, ridges indicated by single lines at large scale only; type 3 spicules not illustrated. Lower right: holotype (USNM 760632) showing body regions measured (A-D) and areas from which spicules were taken (a-h); scale = 8 mm.

four types, keeled distally; type 1 with 3-4 medial and 2-4 lateral ridges extending from base to 3/4 length of spicule; smooth groove between lateral and medial ridges; inner side rounded; type 2 without ornamentation, rounded on outer and inner sides; type 3 proximally like type 1 spicules and distally like type 2 spicules; type 4 like short type 1 spicules except grooved on inner side. *Area g*: 3 types; type 1 dominant, like type 2 spicules of area *f*; type 2 shorter, very thin and flat, with numerous ridges extending 3/4 distance from base, thicker and keeled distally; type 3 (not illustrated) like type 1 spicules of area *f*. *Area h*: nearly all spicules like type 1 spicules of area *g*, but shorter and narrower, most with tips broken (perhaps an artifact); a few spicules like type 2 of area *g* but narrower.

Radula morphology is summarized in Figure 3 and Table 2.

TABLE 2

Radula dimensions and ratios in *Chaetoderma abidjanense* and *C. majusculum* (refer to Fig. 3 for letter designations)

	<i>C. abidjanense</i>	<i>C. majusculum</i>
Total length specimen	18.7 mm	40 mm*
Length cone <i>i</i>	350 $\mu$ m	600 $\mu$ m
Length lateral projection <i>p</i>	140 $\mu$ m	65 $\mu$ m
Length denticle <i>d</i>	24 $\mu$ m	24 $\mu$ m
Length subradular membrane <i>s</i>	300 $\mu$ m	360 $\mu$ m
Frontal width cone <i>i</i>	75 $\mu$ m	130 $\mu$ m
Lateral width cone <i>i</i>	125 $\mu$ m	130 $\mu$ m
Length <i>s</i> : length <i>i</i>	.86	.60
Frontal width <i>i</i> : lateral width <i>i</i>	.60	1.00
Length cone <i>i</i> : total length	.019	.015

\* Specimen stretched; total length approximately same as holotype, the length of body region C (Table 1) being about the same in both specimens.

### Discussion

Both *Chaetoderma abidjanense* and *C. majusculum* are large and stout chaetodermatids with more elaborately sculptured and more types of spicules than are usual for the group. There is little or no overlap in the taxonomic characters used either between them or with other described species of *Chaetoderma*. They would seem to replace the common continental shelf species *C. nitidulum* of the northern hemisphere on the shelf and upper slope off the Ivory Coast.

No representatives of these two species or of *C. nitidulum* occurred in samples dredged off Dakar, Luanda, or Walvis Bay by the Woods Hole Oceanographic Institution, although other chaetodermatid species were present.

### SUMMARY

Two new aplacophoran species from off the Ivory Coast, *Chaetoderma abidjanense* and *Chaetoderma majusculum*, are described by body dimensions and ratios, radula dimensions and ratios, and spicules drawn from light microscope images interpreted by scanning electron microscopy.

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## REFERENCES

- BOETTGER, C. R. 1955. Beiträge zur Systematik der Urmollusken (Amphineura). *Verhandlungen der deutschen zoologischen Gesellschaft 1955, Zoologischer Anzeiger Supplementband*, 19, 223-56.
- HYMAN, L. H. 1967. *The Invertebrates*, 6. *Mollusca*, 1. New York, McGraw Hill.
- SALVINI-PLAWEN, L. v. 1968. Über Lebendbeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia*, 31, 105-26.
- SALVINI-PLAWEN, L. v. & NAPP, H. 1974. Chitin bei Caudofoveata (Mollusca) und die Ableitung ihres Radulaapparates. *Zeitschrift für Morphologie der Tiere*, 77, 77-86.
- SCHELTEMA, A. H. 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere*, 72, 361-70.
- SCHELTEMA, A. H. 1973. Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Zeitschrift für Morphologie der Tiere*, 76, 97-107.
- SCHWABL, M. 1961. *Crystallophrisson* (= *Chaetoderma*) *hartmani*, nov. spec., eine neue Aplacophore aus dem Ostpazifik. *Zoologischer Anzeiger*, 166, 258-277.
- WIRÉN, A. 1892. Studien über die Solenogastres, 1. Monographie des *Chaetoderma nitidulum* Lovén. *Svenska vetenskapsakademiens Handlingar*, 24, 1-66.

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16. Abstract (Limit: 200 words)  The Aplacophora are a spicule-covered, vermiform class of Mollusca important in understanding molluscan evolution and the biogeography and ecology of the deep sea. They first became known to scientists from dredgings made in the waters around Scandinavia in 1844. There are about 300 species described worldwide from all oceans at depths between 10 to over 9000 m with many species still undescribed. Most Aplacophora are less than 5 mm in length, ranging from broad and bulky to narrow and threadlike. There are two taxa: one has a narrow foot upon which they creep, the other has lost the foot and burrows through the sediment. The uniqueness of Aplacophora lies in an external specialized vermiform shape while retaining an internal organization that appears to be primitive. It is proposed that they arose through a process of paedomorphosis which could account for: (1) the small size, vermiform shape, and expression of primitive characters; (2) a plesiomorphic metamerism in Mollusca; (3) a plesiomorphic large pericardium in the primitive classes; and (4) less developed characters in the Aplacophora of a chemically simple cuticle, radula with two teeth per row, small posterior mantle cavity, lack of kidneys, a foot as a nonmuscular ciliated ridge, and joined gonads and pericardium. The classes of molluscs are placed in the sister groups Aculifera and Conchifera. Distributions of aplacophoran genera indicate a pre-Tethyan deep sea radiation. Some species are dominant forms at some localities. Data from deep-sea experimental boxes indicates that one species becomes sexually mature within one year at 1500 m.					
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